The Role of Humour in the Evolution of Hominid Cognition and the Emergence of Language

A thesis submitted for the degree of Doctor of Philosophy

by

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Abstract

This thesis employs a primarily inductive approach to determine the path of emergence and subsequent evolution of humour in hominins based on biological roots. This includes an outline of the cognitive, psychological, and social/behavioural impact ramifications, with emphasis on factors associated with cognitive evolution and the emergence of language and the aesthetic faculty. It is shown that the emergence of humour would have preceded language and prelinguistic humour would have functioned as a "break in pattern" recognition system. This system served the informatic function of detecting and parsing constituent elements of holistic perceptions, and creating abstracted conceptions, which could then be cross-correlated across multiple schemata and manifested in domain-general[1] expressions. Humorous behaviour would have ritualized such expressions, which then became part of shared bodies of knowledge imbued with social capital. Futhermore, due to associated rewards, this system was autotelic and autocatalytic, and thus stimulated the hierarchical evolution of hominin cognition (including the capacity for analogical thought and symbolic communication), behaviour, communication, sociality and culture, before being largely supplanted in its importance by the aesthetic faculty and language, which are shown to be products of this process. As such, humour can be seen to have played an important role in the hominin transition from biological to bio-social evolutionary dynamics.

[1] The domains referred to here are extrinsic in nature. The use of this term will be discussed later (see p.115).

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My sincerest thanks go out to all the people who directly helped to make this PhD thesis a reality. While a comprehensive list is not possible, these intelligent, thoughtful and generous people include Noam Chomsky (for his general interest and encouraging me to turn my ideas into a PhD thesis): Sharon Lockyer (my outstanding primary supervisor); Anton Nijholt, Robin Dunbar, Paul Bahn, Steven Pinker, Dan Sperber, Derek Bickerton, Marc Hauser, Chris Stringer, Douglas Hofstadter, Dan Dennett, Susan Blackmore, Ellen Dissanayake, Mitch Ingram, Francisco Yus, Simon Baron-Cohen, and Stephen Mithen (for their ideas in correspondence); Simon Weaver (for always being kindly and helpful); Richard Talbot and Hauke Riesch (for their helpful suggestions in the examination); many students and staff members at Brunel University; and above all, my loving, patient, and brilliant wife, Nicollette, who makes everything possible and was the most helpful and loving soul through every trial and triumph involved in the process.

Author's declaration

"I declare that, except where explicit reference is made to the contribution of others, that this thesis is the result of my own work and has not been submitted for any other degree at Brunel University London or any other institution."

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1 Introduction

"The world is a comedy to those who think" - Horace Walpole (1842, p.318)

I will begin by breaking with tradition and introducing myself to the reader in an overly familiar manner, while still reassuring anyone more comfortable with conventional academic prose that vast swathes of the stuff will follow very shortly. I am doing this primarily in order to clearly put across the personal hows and whys that underlie the creation of this thesis, but also because the central topic is humour, which inherently involves the violation of expectations, so having something unexpected at the beginning fits well with the subject at hand. Simply put, this thesis maps out the evolutionary origins of humour, and then proposes logical causal evolutionary sequences that would have followed, which eventually led to the emergence of language, art and music in our hominin ancestors.

This may sound rather grand, but initially there was no desire to brew up a grand theory. It simply came about as byproduct of understanding humour in an evolutionary context. The search began because I have worked internationally as a professional comedian for more than three decades (as a performer, a teacher, and a writer, in a diversity of fields including stilt-walking, cartoon voice-overs, stand-up comedy, and video game scripting) and after spending so much time playing watchmaker with the functional dynamics of comedy, I wanted to write a book about stand-up comedy. I soon found that I couldn't explain stand-up without explaining comedy, and I couldn't explain comedy without explaining humour, and eventually, I determined that I couldn't explain humour without explaining its origins and the reasons behind those origins. I found myself aligning with Terrence Deacon's opinion "[k]nowing how something orginated often is the best clue to how it works" (1997, p.23).

As I continued my research I began to see that at its evolutionary root, humour was a self-perpetuating (i.e. autocatalytic[2]) system involving communication and informatics, and from an

[2] In the process of autocatalysis one of the reaction products is also a catalyst for the same or a coupled reaction and as such is inherently recursive.

evolutionary perspective it was evident that it had to have preceded language. The reasons behind these conclusions are discussed in some detail but revolve around the fact that the simplest forms of humour are much less cognitively complex than the simplest forms of language. Humour can exist merely due to violations of expectation in patterns of perception and cognition. It does not have any requirement for conscious expression of symbolic thought(s) or the construtions of a commonly understood syntactic format: "the comical, like the beautiful, can be found ready-made in nature or contrived by human talent" (Berlyne, 2014 p.253). As such, humour can be seen to have been less complex and would have emerged earlier, but significantly, it would have involved the organization of information and the communication of such information, which is crucial to its role as a precursor to language and art.

With the basics of this theory in hand I felt that it was better to pursue a PhD rather than continue with independent research[3]. My curiosity had unintentionally brought me into an area with much broader implications than I had foreseen (or intended). Anyone putting forward a theory on the origin of humour, or the origin of language, or the origin of the aesthetic impulse can expect to be treated as a woolly-headed purveyor of just-so stories and face a high degree of skepticism and criticism. I felt that putting forward a theory encapsulating all three would exponentially increase the level of academic incredulity and that the only way to address this problem was to present the theory with the greatest level of clarity and depth of scholarship I was capable of, and along the way to see if in-depth cross-disciplinary research supported or refuted the ideas I was considering.

During the course of writing the thesis I was intent on finding holes in the essential premises, but for better or worse I found that the more I tried to find holes, the more solid it became. The emphasis was always on producing a scientifically rigorous document. I have done my best to present a clear picture of the topic that is scholarly and scientific rather than romanticized pseudo-science. I have also ensured that it is supported at every possible turn by empirical evidence. What follows is intended to be a work of natural and social science rather than one of imagination, but at the same time it also serves to map out the evolution of the biologically based interdependency between science and imagination.

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[3] A doctoral program offered the benefits of specific demands regarding structure/ format, the support of the academic institution and its members, as well as the credibility yielded by having the research rigorously examined.

This thesis proposes an evolutionary path by which humorous behaviour may have emerged in hominins and then outlines the cognitive, psychological, and sociological impact this may have had. The conclusion that is reached is that the emergence of humour would have served to stimulate the emergence of language and the aesthetic faculty and the dynamics of these progressions are discussed in detail. As will be discussed, evolutionary approaches to humour have typically attempted to identify a single factor that can be seen as the missing piece of an evolutionary puzzle. In contrast, I have taken a more holistic approach and provided a functional account describing the aspects and dynamics of incremental, progressive evolutionary stages and the causality underlying them, and explained how such a progression can be reasonably believed to have evolved from existing faculties observable in higher apes. The reader should be aware that this thesis itself follows an evolutionary path; after the relevant criteria have been determined and defined it describes the proposed evolutionary progression step-by-step, which means that threads such as neophilia and social bonding are followed as the level of overall complexity increases.

What follows is, first and foremost, a work of humour studies rather than one of evolutionary psychology, paleo-linguistics, paleo-anthropology or any other discipline, though research from these fields is given substantial consideration. This is important in the process of considering the text as well as in regards to the broader issue of helping to define the relatively young discipline of humour studies itself. The scope of the research is broad and cross-disciplinary, involving the integration of information/research from multiple academic disciplines within both the physical and social sciences, but humour related aspects are invariably the central hub and this approach was intended to provide a clear and cohesive framework for a complex subject. The broad scope of the research necessarily meant that sacrifices had to be made to keep the word count under control, and as a result some topics I would like to have included or have given greater consideration, such as the emergence of consciousness and the potential of pedagogical and therapeutic aspects of non-verbal clowning, have had to remain in my notes, and I hope to explore these subjects further at a later date.

Central to this thesis is the idea that humour involved communication and the organization of information, and this process yielded rewards and benefits causing it to be self-perpetuating, which led to the exponential progress in the evolution of related aspects. This dynamic recalls Porteus' proposition "humour is not a mere byproduct of human intelligence, but rather that

humour, through its manifestation in smiling and laughing, has contributed to the development of human sociality and so to the evolution of higher-order intelligence in humans" (1989, p.280), but places additional emphasis on the cognitive dynamics involved in the operation of humour.

In relation to cognitive evolution, this thesis decribes how the operation of humour may have helped to create characteristics of the modern human mind, which are partially outlined by Fodor: "what is most characteristic, and most puzzling, about the higher cognitive mind: its ...creativity, its holism, and its passion for the analogical" (1985, p.4).

Chapter 2, ("Methodologies"), provides an outline of the employed methodologies and in Chapter 3 ("Humour theory and evolution") there is a review of the literature of existing general humour theories within an evolutionary context, as well as a review of humour theories that have been specifically constructed in an evolutionary framework. In Chapter 4 ("Definitions"), the preceding review is used to help provide necessary definitions relating to humour, smiling, and laughter, which is followed in Chapter 5 ("Background phylogeny") and Chapter 6 ("Hierarchy of stimuli that elicit smiling/laughter spectrum responses") by a discussion of the general dynamics behind the evolutionary path that led to the emergence of humour, and specific evidence is provided. Chapters 2 through 6 serve to provide the background knowledge required in order to construct a possible evolutionary pathway. This construction begins in Chapter 7 ("Evolutionary stages in early humour") where general causal sequences are proposed and the roles of rewards and benefits in the operation of humour are discussed. This chapter brings together the theoretical aspects already introduced and provides a more specific step-by-step approach wherein it is shown how their presence would have made humour an autocatalytic process that aided in hominins ability to survive and reproduce. In Chapter 8 ("Ramifications of the general use of humour") I continue the chronological progression, elaborate on this picture and map out the continuation of an evolutionary path following emergence to the point when humorous behaviour became common in hominin populations and in all age groups within those populations. This includes a discussion on the effects that general humorous behaviour may have had on sociality, symbolic competence, identities and interactions, neophilia, sexuality and sexual selection, and parental dynamics. This examination provides the background necessary for Chapter 9 ("Secondary ramifications of the general use of humour"), which considers the role of humour in emergence of the aesthetic impulse, specifically, music and the visual arts. The evolutionary path under consideration is completed with Chapter 10 ("The role of humour in the emergence of language") which discusses the role of humour in the origin of language, including

consideration of phonemes, morphemes, syntax, semantics and pragmatics as well as a detailed discussion of Chomskeyan theory and various other origin of language theories. The thesis is then brought to a close in Chapter 11 ("Final Summary") with a summary of conclusions and consideration of broader evolutionary context. The basic idea behind the way the text has been arranged is to paint a clear picture of the actual evolutionary process. The reader can follow a series of logical causal sequences that move the story forward and maintain a strong grounding in behavioural aspects as well as underlying theory.

The original contributions to knowledge within this thesis are broad and cross-disciplinary because the ramifications of the central notions are far reaching. A summary of the more important original contributions to knowledge that are introduced within the text has been included in (see pp.251-253), but the original contributions to knowledge can also be summarized as encapsulating a new explanation for the evolutionary origins of humour, and in so doing providing an evidence-based model that maps out how many of the fundamental aspects of the modern human mind, behaviour and culture evolved from biologically based roots.

2 Methodology

This thesis employs a predominantly inductive approach[4] rather than a logico-deductive one[5] in that it doesn't begin with a theory and the construction of testable hypotheses but instead, reviews relevant data and uses the information derived from that data to formulate a theory. The premises that are discussed in the early sections necessarily involve a degree of speculation, but are shown to be reasonable and logical based on a diversity of related evidence. As such, these premises lead to a series of conclusions that are hypothetical in nature, but are supported by evidence from across multiple disciplines, yielding a holistic understanding of the subject(s).

In keeping with an evidence-based approach, there is an examination of evolutionarily precedent factors related to the homology of aspects constituent in humorous behaviour to determine how humour might have emerged and what qualities it might have had at its point of

[4] It is acknowledged that deduction and abduction are also employed.
[5] For a review of inductive and logico-deductive reasoning see Holyoak, 2005

emergence. From there, it was possible to construct an evolutionary model by extrapolating on the ramifications of general humorous behaviour in various associated contexts: cognitive, communicative, social etc. From this point on, this model is referenced as "the proposed model" and is continually built upon as the thesis progresses. The methodological approach involved the "evolution" of a theory by way of analysis of the process of evolution itself. As such, evolution can be seen to be central to both the topic at hand as well as the applied methodology. It is hoped that this approach has yielded an evolutionary story that is engaging to the reader and provides a easily recognisable progression through a complex subject. In order to provide the reader with clarity and guidance I have provided working definitions of key aspects and given a basic outline of conclusions that follow, but the approach is essentially an inductive one. I believe that this approach yields a comprehensive understanding of this subject with conclusions that are no more probabilistic than those reached through deductive methods. Deductive certainty in relation to subjects such as humour, consciousness, and prehistoric behaviour is illusory because the premises applied cannot be said to be strictly representative of objective reality in a either a qualitative or quantitative sense. No specific systematic inductive approach (e.g. Grounded Theory[6]) has been adopted, but the general premise of reviewing and cross-correlating a diverse body of data in order to construct a theory applies throughout, and this has necessarily led to a high volume of references.

One of the challenges of adopting this type of approach has been maintaining a balance between informed speculation (subjectivity) and testability (objectivity). Clinging too closely to a strictly testable scientific approach when dealing with a topic centred on prehistoric social science severely limits the lines of inquiry that may be taken, but straying too far into the purely speculative presents the risk of producing indefensible just-so stories. Accordingly, while this thesis necessarily contains a measure of speculation, balance is achieved by presenting empirical data whenever possible. Those inclined toward an objective physicalist approach might offer critique as per Popper's post-positivist (or post-empiricist) assertion "In so far as a

[6] Despite my background in comedy practice, I chose not to emply a strict Grounded Theory approach because it would not have been sufficient to provide relevant individual cases, incidents or experiences to develop abstract concepts for all the topics under consideration. Also because the breadth of research required the consideration of theories (as opposed to data) on a wide variety of topics…so it is not strictly "grounded" in data. Similarly behavioural evolution is necessarily conjectural and/or inferential and cannot be built entirely on upon specific data.

scientific statement speaks about reality, it must be falsifiable; and in so far as it is not falsifiable, it does not speak about reality" (Popper, 2005 p.314) and Hempelmann levels this criticism at Hurley et al. (2013) in his review of their book "Inside Jokes" (Hurley et al., 2011), which discusses humour in an evolutionary framework. Following Popper's logic, however, all areas of knowledge that do not offer immediate testability should necessarily be excluded from observation, analysis, and speculation, which is an unproductive approach to both knowledge and science. It is by researching that which is currently untestable that it is possible to determine what relevant testing could possibly be done in the future. Inductive research and speculation on the role of humour in the evolution of human cognition and the emergence of language is helpful in determining what types of testing could be done in relation to relevant genetic material, cultural artefacts and fossilised remains. Furthermore, technological advancements are continually broadening the number of possible testing methods that are available. It is not inconceivable to believe, for example, that advancements in behavioural genetics will become relevant to this research in the foreseeable future (as per Bishop, 2009; Plomin, 2000). In sum, just because the proposed model has aspects that are currently untestable does not mean that these aspects will remain untestable.

The breadth of research involved necessarily resulted in a degree of methodological diversity, which could also be considered to be a specific type of flexible, diverse methodology in and of itself. For example, material relating to the social sciences maintains an essentially anti-positivist stance in that it considers social reality to be something that is created by the individual. This stance, however, works in tandem with an empirical, positivist approach to the biological and ecological aspects underlying the co-evolution of hominin[7] cognition and sociality. As such, the proposed evolutionary model can be seen to partially explain some of the dynamics behind the hominin transition from the biological to the bio-social and as such, the model provides a partial account of the objective, biologically derived origins of subjectivist social reality. In this regard it is also useful to note Bourdieu's proposal that objectivity and subjectivity are not oppositional, but instead, can be seen as operating in a dialectical relationship:

[7] "Hominin," refers to the group consisting of modern humans, extinct human species, and all our immediate ancestors and stands in contrast with the more comprehensive label, "hominid," which includes all modern and extinct great apes eg: modern humans, chimpanzees, gorillas, and orangutans and all their immediate ancestors.

> …on the one hand, the objective structures that the sociologist constructs, in the objectivist moment, by setting aside the subjective representations of the agents, for the basis for these representations and constitute the structural constraints that bear upon interactions; but, on the other hand, these representations must also be taken in consideration particularly if one wants to account for the daily struggles, individual and collective, which purport to transform or to preserve these structures (1989 p.15).

While this thesis is intended as a work of humour studies, it will acknowledge certain tenets and methods adopted within the various disciplines into which it ventures. For example, in relation to evolutionary psychology, the framework of Tinbergen's four questions (1963)[8] has been acknowledged and as a result, there is an examination of the ultimate causes (e.g. adaptive value, evolutionary history) as well as the proximate mechanisms (e.g. neurobiology, development) that resulted in the production of humour. In relation to the sociological aspects of the thesis I will be adopting an etic approach that emphasizes universal aspects of humour rather than the cross-comparison of cultural variants[9]. While this approach does not exclude consideration of aspects of specific cultural examples noted in the literature, the aim is to examine universal sociological processes and dynamics and their possible relevance to an evolutionary scenario.

In concluding the review of methodology I will add that another significant methodological element within the thesis is the referencing of information obtained as a result of my own involvement in various forms of comedy practice. This was found to be primarily applicable in relation to non-linguistic humour (vocal and non-vocal), but aspects relating to linguistic humour have also been referenced. This approach allowed access to a substantial body of information with the advantage of the detail and nuance yielded by practical, phenomenal experience. It should also be noted that autoethnographic[10] aspects of this thesis have been done almost

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[8] Tinbergen proscribes consideration of ontogeny, phylogeny, mechanisms (causation) and functions (adaptation). This incorporates the Proximate - "how" an individual organism's structures function and the Ultimate - why a species evolved the structures (adaptations) it has.

[9] Apte defines an etic framework as "a conceptual model of universal categories developed by an investigator as a methodological aid to research" (1985, p.37).

[10] "Autoethnographic" refers to any content within this thesis that uses personal experience to help provide clarity and meaning to the topic(s) at hand.

entirely in a reflective post-hoc manner and relate to ideas and experiences that preceded the research. As such, they should not be considered to be a primary methodological element, and there were no ethical issues relating to human participants.

This aspect of the methodology is relevant in that creation of comedy material involves a search for alternate viewpoints and the identification of unlikely or unexpected correlates, and being steeped in these dynamics from my years as a comedian, it is only natural that they should become part of my methodology. It has been shown that self-documentation practices in stand-up comedy have specific ritualized qualities and involve the consistent use of varied mnemonic devices (Molineux, 2016). In relation to this, I have employed a somewhat autoethnographic approach and used some of the same documentation practices that I have previously used in documenting my stand-up comedy material such voice to text, and hand-written notes with the use of semiotic elements, but took note that typing material on a computer was far more prevalent for pragmatic reasons. While I did not formally record or study the documentation practices I employed during the course of this thesis I believe that a cross-comparative study of creative approaches and documentation practices in comedy and academia would be of value. In broader terms, the approach that was used can be seen to be reflective of humour in that it necessitated aspects of arousal and neophilia: it was an energetic search across varied academic terrain that involved darting down many novel pathways and considering all options from a fresh perspective. It is perhaps appropriate that humour theory regarding evolution should, itself, evolve.

It is possible that, based on the nature of the subject and the background of the author, the reader might expect examples of humour to be generously peppered within this thesis. This, however, is not the case. I felt that while the pedagogical potential of humour is noteworthy, in the context at hand it was more prudent to apply humour sparingly. Creating a work that could be seen in any way as comical, would have the potential to undermine the validity of the research in the eyes of many academics. Such risks have been noted in relation to a variety of academic pursuits (Pinto & Riesch, 2017) and more specifically in relation to teaching science (Fisher, 1997; Lei et al., 2010), and it has also been documented that academic papers with

humorous titles receive fewer citations (Sagi & Yechiam, 2008). It could be argued that I have overcompensated in this regard and, as a result, produced a work of daunting academic density, but I am willing to accept that criticism. The reason behind this was to demonstrate a sufficient depth of scholarship in what is necessarily a very cross-disciplinary work. This approach involves the occasional inclusion of fairly detailed technical information drawn from numerous disciplines, which makes the thesis a less approachable document, but one that is, in the author's opinion, sufficiently academically rigorous. While this approach might disappoint scholars who crave a sizeable dose of amusement in their readings, I would kindly suggest that PhD theses are perhaps not the best hunting ground for large doses of amusement. Fortunately, many other avenues of hilarity are available for these good natured souls to sate their comic palate.

3 Humour Theory and Evolution

Theories of humour in an evolutionary context can be divided up into two categories: i) general theories considered in an evolutionary context and ii) theories that specifically incorporate an evolutionary framework. I will briefly discuss a number of theories in both categories. The purpose of the following section is to provide an overview of existing theories and their primary constituent ideas, which will help to provide the necessary framework within which analysis of evolutionary aspects relating to humour can then be done. To provide an easily navigable framework, general theories of humour will be considered within a tripartite classification of mental activities: Cognitive, Affective, and Conative (as per Eysenck, 1942 and Flugel, 1954) (for an overview of this classification system see Hilgard, 1980). This approach is useful in parsing aspects of humour creation and appreciation, which can then be considered in an evolutionary context. The consideration of humour theories also provides a general overview of humour, and is useful in helping to construct a working definition for the term "humour". It is also worth noting that this thesis, by default, could be considered to construct a distinct theory of humour, though that is not the intention, and any such interpretation would only be applicable within the evolutionary context under consideration.

3.1 General humour theories

Humour has been the subject of speculation and theorizing since the time of Aristotle and in contemporary summaries the primary theories are typically classed as: Incongruity (or

Incongruity/resolution), Superiority, Tension Release, and Mechanical[11] (e.g. Hurley et al., 2011) but these will be subsumed within a framework which applies the terms Cognitive, Affective, and Conative because these are terms commonly used in psychology, which makes them more practical within cross-disciplinary study. For example, these terms facilitate consideration of neurological aspects, and while this thesis will not attempt to present an organized analysis of the neurology of humour, it will make reference to relevant neurological aspects as topics are discussed. Due to the multiple complexities involved in humour creation and appreciation (neurological, psychological, behavioural, social etc.) these terms are necessarily reductive (e.g. it can be argued that cognition involves affective and conative elements) but they remain practical for the topic at hand and the "Cognitive", "Affective" and "Conative" subsections will be prefaced with definitions of each term taken from the same source: (Huitt & Cain, 2005). It is also notable that humour can be divided into objective and subjective categories: in terms of the stimulus or in terms of the perception/interpretation/response (Scheerer, 1966). This thesis considers the term "humour" to encapsulate both categories and objective and subjective aspects will both be given some consideration.

As the term "cognitive evolution" implies, our hominin ancestors did not possess the same mental architecture, abilities or related social structures as contemporary humans and it is therefore appropriate to attribute more simplistic forms of humour appreciation/creation to them. This necessarily restricts the applicable definition of humour because it eliminates the relevance of theories that are dependent upon more evolved cognitive operations such as language e.g. The Script-based Semantic Theory of Humor (Raskin, 1985) and The General Theory of Verbal Humor (Attardo & Raskin, 1991). The following section serves the dual function of providing a literature review relevant to humour in an evolutionary context while also providing framing for the further consideration of the subjects that follow.

Cognitive

"Cognition refers to the process of coming to know and understand; the process of encoding, storing, processing, and retrieving information. It is generally associated with the question of

[11] Mechanical refers to Bergson's notion of the mechanical encrusted upon the living; the person as object.

"what" (e.g. what happened, what is going on now, what is the meaning of that information.)" (Huitt & Cain, 2005 p.1).

As cognitive evolution is central to the topic at hand, cognition is a good starting point for the terms under consideration, which otherwise, are presented in no particular order. At a general level the importance of the relationship between humour and cognition is well illustrated by Brone et al.'s statement "(t)he study of humor can yield interesting insights into some of the specifics of cognitive processing" (2006, p.205). Existing cognitive theories of humour typically relate to the principle of incongruity, the cognitive dynamics of which can also be considered in a Gestalt framework[12]. Incongruity theory asserts that humour results from perception/cognition involving an unusual and/or unexpected juxtaposition of two or more events, objects, ideas and/or other mental schema. This has been defined by different scholars in different ways e.g. "(i)ncongruity of the joke's ending refers to how much the punch line violates the recipient's expectations" (Suls, 1972 p.92); "(i)ncongruity is usually defined as a conflict between what is expected and what actually occurs in the joke" (Shultz, 1976, p.12). Schopenhauer provided a definition with slightly more context when he stated "(a)s a rule, laughing is a pleasant state; accordingly, the apprehension of the incongruity between what is conceived and what is perceived, i.e. reality, gives us pleasure, and we gladly give ourselves up to the spasmodic convulsion excited by this apprehension" (1958 p.98). Some incongruity theories specifically incorporate an element of "resolution" (i.e. cognitive integration or understanding) (e.g. Koestler, 1964; Ritchie, 1999; Rothbart & Pien, 1977), and Shultz (1976) believes that this also occurs in tickling games, which suggests the possibility of an early phylogenic origin for the element of resolution. Incongruity theory overlaps with theories that involve suddenness/surprise (e.g. Sully, 1902), and ambivalence (e.g. Eastman, 1921), though in the case of ambivalence there is an additional affective element involved due to the requisite cognitive interpretation of emotional elements.

Incongruity theory is the most generally accepted humour theory (Morreall, 1987; Oring, 2010) and despite difficulties associated with the fact that the presence of incongruity does not ensure humour (Kozintsev, 2011; Martin, 2010) (there are many incongruities that are not funny), there is general acceptance that incongruity is a prerequisite of humour (Hurley et al., 2011; Martin,

[12] Consideration of a Gestalt framework follows on p.20.

2010). In considering incongruity theory in an evolutionary context it is necessary to acknowledge that the element of expectation, which is central to incongruity theory, is dependent on the faculties of memory, perception, and cognition and as a result these topics are worthy of further consideration.

The notion of incongruities has ramifications in terms of the cognitive functioning it requires. To begin with, incongruities can also be considered as "breaks in patterns" because incongruity requires expectation, which necessarily involves sequences of perception and cognition, which constitute patterns. It is also significant that the volitional creation of humour is not only a cognitive process, but also a metacognitive one because it involves the cognitive cross-correlation and evaluation of information (of input derived from perception and/or memory) relative to mental representations held within memory: it involves thinking about thinking. As such, the emergence of general humorous behaviour in hominins would have involved conceptual, rather than purely perceptual, thought as per Mantonakis et al.'s (2011) description of Whittlesea's SCAPE (Selective Construction And Preservation of Experiences) model of memory (1997): "The effects of prior experiences on current behaviour do not simply involve retrieval of a mental representation, but also pertain to the contextually driven subjective quality of that retrieval" (p.41). This cross-correlative aspect can be related to the notion of conceptual integration (sometimes referred to as "blending") proposed by Fauconnier and Turner (1998)[13], the notion of cognitive fluidity proposed by Mithen (1996), as well as more general notions of modularity and meta-cognition (e.g. Carruthers & Chamberlain, 2000; Sperber, 2001), and recursion. It also is notable that Deacon's description of recognition matches the description of the cognitive process involved in humour: "(r)ecognition means the linking of something new to something already known" (1997, p.93), but in the case of volitional humour it can be also seen as making something new out of something already known.

Bearing this in mind, it can be seen that the experience of humour creation typically involves a metacognitive process of contextualization between current experience and mental representations held within memory. The voluntary creation of humorous expressions involves the contextualization of actions, objects, or ideas in relation to mental representations derived

[13] This connection between Fauconnier and Turner's conceptual integration theory and humour has been noted by Dynel (2011).

from previous experience and as such, involves cognition regarding the process of cognition, thought about thought: metacognition. Taking this line of inquiry one step further, it can be seen that humour involving creation by one party and appreciation by another, involves social meta-cognition (cognition relating to the mental representations and emotions of others), which is more commonly referred to as Theory of Mind (Galese, 2007). As such, the majority of humour involves the cross-correlation of mental representations not only within individuals but also assumes (or predicts) the mental representations and their related emotional states in others[14].

Another cognitive approach to humour has been to frame it in terms of Gestalt ideas (e.g. Maier, 1932). This can be considered as an extension of incongruity theory where the mental representations demonstrating incongruity are considered within a Gestalt framework. A gestalt refers to a unified mental notion that results from the perception/cognition of multiple contributing factors. It represents a holistic mental interpretation derived from definable cognitive/perceptual elements that is different (rather than greater) than those elements (for a basic overview see Sabar, 2013). From a Gestalt perspective, humour involves sudden perceptual or cognitive shifts from one gestalt to another, so again the potential for elements of suddenness, surprise, and ambivalence can be seen. Gestalt principles in humour are well illustrated by incongruity within background/foreground images, which are a commonly referenced in Gestalt psychology.

While Gestalt humour theory can be considered merely as a subset of Incongruity Theory, it does provide a fairly detailed framework which has been applied in humour studies (e.g. Cori et al., 2016). Another similar deconstructive approach that could be applied in this regard is Feature Integration Theory (Treisman & Gelade, 1980), which comes from the field of cognitive psychology and proposes that cognitive processing involves the perception of specific, separable features that are then integrated into a complex whole. Beyond questions of the veracity of Gestalt theory in general it is worth noting that Incongruity Theory can be applied to a cognitive theory relating to mental representations and subsequently extrapolated therein. In the context of cognitive evolution, it can be seen that the operation of humour would have involved the cross-correlation of multiple mental representations, Gestalt or otherwise, in a social context. As such it is reasonable to believe that continued humorous behaviour would have

[14] Theory of Mind will be discussed in some detail at numerous points during the course of this thesis.

served to gradually strengthen, clarify and evolve the mental representations involved, and would also have shared them within social groups.

Affective

“Affect refers to the emotional interpretation of perceptions, information, or knowledge. It is generally associated with one’s attachment (positive or negative) to people, objects, ideas, etc. and asks the question "How do I feel about this knowledge or information?"” (Huitt & Cain, 2005 p.1).

In the preceding definition[15] Huitt and Cain use the word “interpretation”, implying a cognitive act, which arguably, does not fall within Huitt’s and Cain’s definition of “cognitive” (see p.18). As such, affect can be seen as the cognitively mediated processing of emotion(s), but it remains differentiated from cognition proper because it is predicated by emotions, which Izard defines as “specific neuropsychological phenomena, shaped by natural selection, that organize and motivate physiological, cognitive, and action patterns that facilitate adaptive responses to the vast array of demands and opportunities in the environment” (1992 p.561). Once again, cognition is included as part of the operational dynamics of emotion, and the interrelationship between emotion and cognition has been the subject of much study (for a review see Lazurus et al., 1980).

In discussing humour in an evolutionary context, Hurley et al. asserted that all thought is predicated on emotion, which they define as “an internally induced pleasure or pain – a valenced perception – caused by a variety of processes of transduction of information in the world” (2011 p.72). It is not necessary to determine the veracity of this claim, but even if emotion were to be accepted as an essential constituent of the cognitive process, this does not mean that the relationship is necessarily a causal one, and this is generally considered not to be the case (Lazurus et al., 1980). Emotions involve motivations but not motives, motives being something that require cognitive articulation. In addition to this, from a psycho-evolutionary standpoint there is some debate as to the validity of the term “emotion” itself: “emotions do not

[15] It is acknowledged that the definition of affect used differs from that typically used in Affect Theory in the humanities, which is more concerned with social dynamics and non-linguistic communication, but a more comprehensive consideration of the term is not warranted.

form a natural category because they lack a common underlying mechanism" (Lazurus et al., 1980 p.191). It is not necessary to resolve this issue here, but the debate on this topic helps to underline the tenuous nature of theories based strictly on emotion.

Bearing in mind the preceding, affective humour theories can be thought of as those that are predicated upon emotional states and dynamics. In practical terms it is sometimes possible to clearly differentiate cognitive and emotional responses to humour. As a stand-up comedy performer I have often experienced individuals and crowds laughing at specific instances of humour due to the prevailing emotional state and then correcting themselves as they process the meaning behind the joke, because they have determined there is an aspect (or aspects) that they deem to be inappropriate. Humorous behaviour can be said to involve what Paulos calls an "appropriate emotional climate" (1980 p.10) and this notion is supported by Sroufe and Wunsch's assertion that "context and stimulus may be inseparable" (Kozintsev, 2011, p.86, cf: Sroufe and Wunsch, 1972). In his "Optimal Arousal Theory" Hebb concurs with this view and adds to it the notion of arousal, proposing that humour is most typically associated with a combination of pleasant hedonic tone and moderate arousal (1955). This can be coupled with the common sense notion that humour is indicated the presence of smiling and laughter, which are emotional expressions. As such, humour can be seen to have essential emotional elements.

It is notable that while there are humour theories that put primary emphasis on emotion and exclude the element of incongruity such as McDougall's notion that laughter is a type of emotional anaesthetic (1903) [16], the majority of affective theories reference dynamics that can be related to incongruity. Examples of this include the surprise theories of Hartley (1775) and Descartes (1989), and Veatch's characterization of humour as "affective absurdity" (1998, p.161). Incongruity also plays a role in ambivalence theories, which propose "laughter results when the individual simultaneously experiences incompatible emotions or feelings" (Keith-Speigel, 1972 p.10). This can be seen to involve incongruity referred in relation to "emotions or feelings" rather than mental representations: a cognitive process determines the requisite incompatibility.

[16] McDougall's notion of humour as an emotional anaesthetic is not being endorsed here, but merely cited to provide broader context for the consideration of the role of emotion within humour theories.

From an evolutionary perspective the consideration of the emotional component of humour is significant due to the ancient evolutionary origins of emotion. It has been claimed that emotions are actually panphylogenic i.e. they exist in some form in virtually all organisms (Plutchik, 1982). This evolutionary frame stands in contrast to the discussed notions of the metacognitive cross-correlation of mental representations and Theory of Mind, which are limited to humans and possibly a small number of higher apes (Heyes, 1998; Premack & Woodruff, 1978). This implies that it was the evolution of the cognitive aspect that was instrumental in the emergence of humour, but the ubiquity of emotion in humour and the inter-relations between cognition and emotion show that consideration of the emotional components of humour (and related arousal) is essential in understanding humour in an evolutionary context.

Conative

"Conation refers to the connection of knowledge and affect to behavior and is associated with the issue of "why." It is the personal, intentional, planful, deliberate, goal-oriented, or striving component of motivation, the proactive (as opposed to reactive or habitual) aspect of behavior (Baumeister, Bratslavsky, Muraven & Tice, 1998; Emmons, 1986). It is closely associated with the concept of volition, defined as the use of will, or the freedom to make choices about what to do (Kane, 1985; Mischel, 1996). It is absolutely critical if an individual is to successfully engage in self-direction and self-regulation." (Huitt & Cain, 2005 p.1).

In hierarchical, and thus evolutionary, terms, conation is more complex than both cognition and affect in that it incorporates the correlation of both cognitive and emotional elements. Maslow's (1943) idea of conation as an element in cognition is important in an evolutionary context because he asserts that this relationship is specific to modern humans[17]. Conation in modern humans differs from conation in other animals in that it is conscious and voluntary (Bandura, 1997) and it is more commonly considered in relation to behaviour rather than cognition.

Simply put, conative humour theories are those that propose the centrality of a strategic behavioural element, and the most prevalent of these theories is Superiority Theory. Superiority Theory proposes that humour provides a way for individuals to feel superior to others by making

[17] The term "modern humans" here refers to those hominins whose level of cognitive development can be seen to be substantially the same as contemporary humans.

them ridiculous, and it is nicely summed up by Gruner: “(w)hen we find humor in something, we laugh at the misfortune, stupidity, clumsiness, moral or cultural defect, suddenly revealed in someone else, to whom we instantly and momentarily feel ‘superior’ ” (1997 p.6). Superiority Theory goes as far back as Aristotle, who described comedy as “an imitation of characters of a lower type” (2006 p.1) and 1800 years later the idea was still thriving when Thomas Hobbes proclaimed, "laughter is nothing else but sudden glory arising from some sudden conception of some eminency in ourselves” (1999 pp.54-55). Superiority Theory has fallen out of favour in the past century because it refers to a motivation rather than a mechanism, and because there are many humorous instances where it does not apply: naïve humour, abstract humour etc. For example, take a simple joke like Q: what's white, wears a tartan jacket, and can't climb trees? A: Rupert the fridge. This joke doesn’t serve to produce any great wave of sudden glory, but it does display incongruity.

While conative aspects of humour are not generally considered sufficient to constitute a general theory of humour (Martin, 2010), their presence in humorous behaviour is well documented (e.g. Duncan, 1985; Francis, 1994) and can be applied in an analysis of behaviour and social dynamics in an evolutionary context. As such, the role of conation in conscious, voluntary communication as per Bandura (1971) is also of particular interest in relation to hominin evolution. It is also notable that Social Identity Theory (Tajfel & Turner, 2004), which proposes that people categorize themselves and others based on abstracted prototypical characteristics, has been studied in relation to conative aspects of humour (e.g. Bourhis et al., 1977; Ferguson & Ford, 2008), and this is significant in relation to the topic under consideration[18].

Synthetic

A synthetic theory is one that involves the integration of the three elements that have been discussed. The majority of humour theories typically incorporate some degree of cognitive, affective and conative aspects (Eysenck, 1942; Martin 1998), and when a theory is referred to as a “Cognitive Theory” or a “Conative Theory” this simply indicates where the primary emphasis of the theory lies. It has already been asserted that all conative theories are necessarily synthetic in nature, and neurological research supports the idea of a synthetic approach as cognitive and affective pathways have the ability to influence each other

[18] There is further discussion on this topic on p. 138

reciprocally (Azim et al. 2005; Otto, 1994). There have also been occasions where all three aspects have been explicitly acknowledged in humour theories (e.g. Flugel, 1954; Hurley et al., 2011; Ramachandran, 1998). A good example of a synthetic approach can be seen in Relief Theory (for a summary see Martin, 2010), which proposes that humour is a way of releasing psychological tension caused by repressed thoughts and feelings. It is true that humour involves the cross-correlation and reconfiguration of mental representations and the resulting laughter is a reflexive convulsion that results in the expenditure of energy, and as such it could be argued that this constitutes a release of tension, but supporting clinical data in this regard is lacking (Dienstbier, 1995). A central problem with relief theories lies in the notion of "tension" itself. Hurley et al. (2011) address this when they ask "why would one build up a special reserve of a strange kind of energy, and where would one save it, instead of simply dissipating it in the first place?" (p.44). One legitimate aspect of Relief Theory is that it can refer specifically to stress release, and the positive correlation between humour and stress release is well documented (e.g. Abel, 2002; Lefcourt & Martin, 2012) and worthy of consideration as a factor in evolutionary terms.

3.2 Evolutionary theories of humour

Having examined ideas and information relating to the basic cognitive, psychological, and social dynamics underlying the creation and appreciation of humour, it is now possible to look at how these have been applied in theories relating to humour in an evolutionary context. There have been a number of examinations of humour in an evolutionary context. Some of these have been brief speculations (e.g. Provine, 2001) while others have involved a more detailed analysis (e.g. Gervais & Wilson, 2005; Hurley et al., 2011). I will give a brief outline of some of the existing evolutionary theories of humour here, but will only offer limited detail and critique at this point. Further analysis and critique is most productively presented as counterpoint to specific ideas as they emerge in the course of this thesis, and so the different theories will be considered in more detail if and when they become relevant.

It is generally accepted that laughter and smiling are closely associated with humour even if this association is not necessarily absolute (Kozintsev, 2011). Bearing this in mind, from an evolutionary perspective it can be seen that humour had to have emerged either a) as the result of a homologous progression from earlier forms of laughter/smiling stimulus or b) in an analogous fashion, where the previously existing faculties of laughter and smiling (Preuschoft &

van Hooff, 1997; Ross et al., 2010) were co-opted as elements within the distinct cognitive/emotional system of humour. Even though the former explanation might instinctively appear more plausible, there are evolutionary humour theories that have favoured the latter approach (e.g. Miller's Sexual Selection Theory (1998)). This is because the researchers are proposing a singular adaptive function for humour and this results in a theory than runs roughly as follows: humour can be seen to produce effect "a", and effect "a" would have had great adaptive significance, so it is proposed that effect "a" explains why humour emerged. In the case of Miller's theory, the line of thought is: humour is useful in communicating a higher level of intelligence, is metabolically expensive to produce, hard to maintain, and not easy to counterfeit, and as a result it is a reliable indicator of genetic fitness, so it emerged in hominins because they could capitalize on this adaptive value. This approach is problematic because it fails to address the finer mechanics of how and why emergence might have occurred: why would this new form of stimulus have simply produced laughter and smiling without any homologous line of development? Without an associated holistic, evidence-based causal chain, any evolutionary theory becomes pure speculation. In short, while failing to present a broader context, this approach is not necessarily displaying faulty logic in relation to the functional dynamics of humour in an evolutionary context, and considering such theories might help to explain why humour proliferated and continued to evolve, but they do not explain how and why humour might have emerged.

In conclusion, it is logical to assume the possibility that humour may have been the culmination of the gradual homologous evolution of forms of stimuli for smiling and laughter and as such, the topic must be considered and either accepted or rejected before adopting an analogous approach. If a specific path of homologous evolution is seen to be possible, there is still the potential for adaptive values that have been identified in homologous and/or analogous theories to be associated with that path.

I will now move on to a brief review of some of the existing literature that involves evolutionarily based humour theories.

The joy of debugging

As was just mentioned, speculations about humour in an evolutionary context typically involve the advocation of a single prime adaptive benefit. In the case of Hurley et al.'s 2011 book

"Inside Jokes", one of the more detailed works on the subject, the proposed adaptive benefit is Hurley's notion of "the joy of debugging" (2006). Hurley et al. assert that humour

> encourages the process that keeps data integrity in our knowledge representation. This process ensures that we reduce the likelihood of making faulty inferences and fatal mistakes. Without a trait like this, a cognitive agent as complex as we are would be practically guaranteed a quick death (2011 p.289).

To some degree this theory draws from Suslov's proposal that humour represents "a specific malfunction in the course of information processing conditioned by the necessity to delete some information transmitted to consciousness" (1992 p.1) though he puts equal emphasis on the speed of this information processing and ascribes adaptive value to both aspects. The problems of attributing a single adaptive function to explain the existence of humour have been mentioned and are supported by Hempelmann in his review of Inside Jokes: "humor as a property of texts, a cognitive process, a character trait, an emotion, a world view, a cultural variable is far too complex to assign a single function to" (2013 p.1). While the argument to accept "debugging" as being of particular adaptive value is persuasive, one still has to ask, why not consider a synthesis of the totality of possible adaptive benefits? They have pointed out a single adaptive trait but not considered the subject from a more integrated, holistic standpoint, or comprehensively examined what impact (cognitive, communicative, social etc.) the operational dynamics of humour would have had in a pre-modern context.

Another shortcoming in Hurley et al.'s model is its distorted view of evolutionary dynamics, an example of which can be seen in the following passage: "Mother Nature—aka natural selection—cannot just order the brain to find and fix all our time-pressured misleaps and near-misses. She has to bribe the brain with pleasure" (Hurley, Dennett and Adams, 2011). This is more than just casual and careless use of language, it changes the framework within which the subject is researched and understood. While Hurley et al. are not promoting some form of intelligent design with "Mother Nature" as the creator, the language they are using is misleading and reflective of (and possibly the cause of) mistaken direction within the research. Natural selection is not a decision-making rational entity and species certainly do not acquire traits because they "need" them. Just because it is possible to observe logical structures in examples of the evolutionary process does not mean that logic is being actively employed. It is simply a process by which the components of the universe, by obeying the laws of physics, interact and

produce novel reconfigurations, which are then subject to selective pressures. In addition to this, this approach tends to stimulate the desire to find "the reason" for something rather than to parse out aspects of reason within the system as a whole. As a result, Hurley et al.'s approach produced research that tried to determine why evolution "created" humour for us, and/or why we might have "needed" humour. As a result, having identified the single plausible adaptive benefit of debugging, the search was considered to be over and they packed up their analytical tools and went home. Hurley et al. failed to give a detailed consideration of possible early forms of humour and/or the possible hierarchical stages of progression and the importance of such consideration is summed up briefly and eloquently by Sylvia Bliss (1915) in "The Origin of Laughter" where she states:

> to perceive certain ends which a function serves is by no means to account for its existence. It is evident that the laughter of the modern human being is a highly complex function far removed from the bald simplicity of that first laugh whose strange sound broke the long, silent gravity of the pre-human ages (p.237).

Gruner's Superiority Theory

Superiority Theory was already briefly discussed and Gruner framed it in an evolutionary context (1978, 2000). He considered humour in modern humans to be a form of "playful aggression" that had its origin in more genuinely violent roots. He hypothesized that after defeating an opponent in violent combat, our ancestors were compelled to bare their teeth and pump their shoulders (as a dominance display), and separate their breath into small laughter-ish grunts which performed a homeostatic function (1978). Aside from the dubious adaptive value of such a homeostatic function and the fact that there is little to no remnant of such behaviour in modern humans (boxing matches and military conflicts are not rife with reflexive laughter), this theory is problematic because of the proposed analogous evolutionary path. Smiling and laughter would have already existed as a product of tickling as is shown by its presence in apes (Ross et al., 2009), so how and why would it have been co-opted for the proposed purpose? Gruner cites Koestler's work (1964) discussing tickling, but only to place it in the behavioural framework of being seen as "mock attack" (2000 p.151). The stimulation of smiling and laughter through tickling involves a physical cause and effect reflex (Carlsson et al., 2000), and Gruner fails to address how or why the smiling and laughter came to be stimulated by completely novel cognitive/affective means (i.e. there is no physical cause and effect), either homologously or

analogously. Gruner's theory addresses behavioural aspects on the response side, but does not adequately explain its emergence, or operational mechanisms.

False Alarm Theory

The basic premise of the neuroscientist V.S. Ramachandran's False Alarm Theory (1998) is similar to ideas put forward by Hayworth (1928) and Lorenz (2002), and it is the idea that laughter, and thus humour, was produced "to inform conspecifics that there has been a 'false alarm', to which they need not orient" (Ramachandran, 1998 p.351), and Ramachandran goes on to add that "this model accounts for the evolutionary origin of laughter" (1998 p.352). False Alarm Theory incorporates elements of both incongruity and ambivalence but posits a specific motivational aspect that is cognitive, affective, and conative in nature. In some ways Ramachandran's hypothesis is similar to Gruner's, but in False Alarm Theory the proposed adaptive value is based in communication rather than homeostatic regulation: "I suggest that the main purpose of laughter is for the individual to alert others in the social group (usually close relatives that are likely to share the same genes) that the anomaly detected by that individual is of trivial consequence" (1998 p.352). As with Gruner, a single adaptive function of questionable value is proposed. In discussing False Alarm Theory, Morreall gives a theoretical example:

> A band of early humans is walking across the savannah, when they spot a lion in the clearing ahead. They freeze in their tracks for a moment, but then they see that the lion is feasting on a zebra and doesn't even look up at them. With the sudden realization that the lion is not a threat, they laugh, signalling to each other "We're safe. We can enjoy this" (2011 p.43).

This is a far from convincing scenario, in fact, it is not unreasonable to propose that a group of hominins spontaneously expressing a noisy convulsion next to a feeding lion may have altered their chances of survival in a negative way. It is also notable that laughter in modern humans is not typically elicited in situations involving false alarms: finding a lost wallet in a back pocket, realising you didn't forget to mail an important document etc. From my own professional experience I can attest that in terms of comedy performance, this is not a dynamic that is typically employed or observable. Creating a sense of threat and then alleviating that threat might function comedically in a few specific circumstances, but in a general sense would be more likely to create a general mood that would not be conducive to laughter. The

comedian/magician The Amazing Jonathan employed a danger/release dynamic in the opening of his routine at the 1995 Just for Laughs festival where he pushed the microphone stand so it looked like it was going to fall on someone in the front row, then at the last moment he stepped on the base and it popped back to its normal position. Significantly, it can be seen that this example was primarily effective with observers of the event rather than the person/people who was threatened, which shows it to be more demonstrative of Superiority Theory. Within the same performance he used danger/release dynamic again, typically showing a threat to himself and then alleviating it, and this is also the centrepiece of almost all comedy in sword swallowing routines. Again, this can be seen to be more indicative of a Superiority dynamic, and offers further evidence against the viability of the dynamic proposed by Ramachandran.

Ramachandran also surmises that False Alarm Theory is applicable in tickling: “(t)he adult approaches the child menacingly with his hand stretched out. 'Will he shake me or poke me or hurt me in any way?' asks the child's mind, only to learn no, the finger makes only light intermittent contact with my belly.” (1998 p.353). This scenario is somewhat inventive in its choice of words. Adults tickling children do not usually approach them “menacingly” and it implies that if someone knew they were going to be tickled by someone aggressive they could simply choose not to laugh, which is not the case (Mintz, 1968). Furthermore, it has also been shown that “simply the threat to tickle can serve as a conditioned stimulus” (Provine, 2000, p.125), so the threat, rather than its alleviation can be seen to be the stimulus for laughter. Ramachandran’s proposed tickling scenario also fails to meet his own specified criteria of serving to “alert others in the social group” as tickling does not require a crowd of witnesses in order to elicit laughter (and neither does humour). Overall, False Alarm Theory assumes the emergence of the laughter/humour to have been predicated on a dubious single adaptive value and the proposed dynamics are rarely observable, let alone universal.

Other evolutionary humour theories

Laughter and humour have also been considered in an evolutionary context within other behavioural frameworks which necessarily incorporate cognitive, affective and conative aspects. Examples of this include:

1) Dunbar’s claim that “laughter (as a form of wordless, amusical chorusing) evolved very early during human evolution as a way of increasing the size of the grooming group”

(2017, p.210)

2) Miller's proposed role for humour into the process of sexual selection, which is summed up by Kaufmann et al: "there is a competition to mate with individuals who exhibit traits such as humor that are (in theory) metabolically expensive to produce, hard to maintain, and not easily counterfeited, because these qualities will be the most reliable indicators of genetic fitness." (2008 p.232).
3) Charles Darwin's proposal that laughter functioned as a social expression of happiness, which caused social cohesion resulting in a survival advantage to the group (1998).

The preceding represents a very brief overview of ideas within the existing literature, and these and other scholarly ideas relating to humour in an evolutionary context will be referenced consistently throughout this thesis. In sum, evolutionary theories of humour have suffered from a focus on attempting to identify a single specific adaptive value to explain the emergence of humour. There has been very little consideration of the specific dynamics of humour creation beyond the attribution of the proposed adaptive value(s), let alone an attempt to map out a causal chain resulting in a gradual evolutionary path for humour creation, and the cognitive, psychological, and social ramifications of such a progression. These errors will be borne in mind within this thesis, and such errors will be avoided. As a starting point to mapping out the evolutionary emergence of humour, it is logical to believe that the laughter and smiling typically produced by humour is homologous to that produced by tickling rather than being representative of a seperate, unrelated process, therefore the origins of humour should be considered and rejected in light of this, before pursuing the notion of an analogous origin.

4 Definitions

Having provided a brief summary of existing humour theories in an evolutionary context I will now move towards determining a likely evolutionary origin for humorous behaviour by examining relevant background aspects of a possible homologous scenario. Before embarking on this it is necessary to address matters of semantic hygiene and provide specific definitions for a few important terms that will be referred to throughout. The following is intended to provide clear parameters for the relevant terms rather than serve as a detailed analysis of associated ideas.

4.1 Defining humour

The term “humour” is being used in this thesis because it is the most common appropriate term within the framework of contemporary academic discourse. Despite Caron’s opinion that “‘humor’ is tangled in a very specific and elaborate history of use in western discourse which renders it problematic as an umbrella term for the situations and artefacts which make all people laugh” (2002, p.246), the term is generally accepted within academia (e.g. Hurley, Dennett & Adams, 2011; McGhee, 1979; Martin, 2010; Meyer, 2000; Fry, 1994) and it is sensible to use it for the research at hand.

The definition of humour is something of a conundrum in the context of this thesis because the act of mapping out the origin and evolution of humour has the potential to contribute to a more accurate and comprehensive definition of humour than currently exists, but the process cannot begin without providing a definition of humour itself. This conundrum can be partially resolved within the context of a homologous origin, which would assume that humour is a complex process derived from specific definable biological roots. In this type of scenario there would have been a gradualistic hierarchical evolution that would have reached a certain threshold after which it could be considered that proscribed criteria for “humour” would be met if the definition were relatively general in nature. So it can be seen that a general definition will suffice at this point.

The required definition only needs to define humour at its point of emergence, which means that it will necessarily differ from most extant definitions, which refer to humour in its present (evolved) state. Perhaps the most important aspect of this distinction is the fact that it must exclude language-based aspects. Despite the immense variety of documented non-linguistic humour: physical (clowns, mimes etc.), humorous objects and art, sounds and music etc. (e.g. Dalmonte, 1995; Kemnitz, 1973; Norrick, 2004, Poyatos, 1992), there have been many attempts to define humour based on language. Some, such as Monro’s (1988) definition, which states that the term humour in the broad sense “is applied to all literature and to all informal speech or writing in which the object is to amuse, or rouse laughter in, the reader or hearer” (p.349), simply avoid any reference to non-verbal humour. Other definitions, such as Attardo and Raskin’s General Theory of Verbal Humour (GTVH) (1991), adopt verbal models because they offer the benefit of providing a detailed structure suitable for analysis, but they do not specifically deny the existence of non-verbal humour.

Referring back to the preceding review of humour theories, there are a few basic elements that can be reasonably incorporated into a loose definition of humour that is suitable for the task at hand.

1) An element of incongruity, i.e. breaks in patterns of expectation.
2) An appropriate emotional climate.
3) A moderate level of arousal.
4) The stimulation of smiling and/or laughter.

These four elements help to provide a framework for an applicable definition but it is worthwhile to consider, contrast, and ultimately integrate objectivist and subjectivist aspects as per Kosintsev's (2010) observation that humour can be defined in terms that are "objectivist ("stimulus-side"), subjectivist ("response-side") and relationist ("whole process")" (p.24). In keeping with an inductive methodology this thesis assumes a relationist position that examines the totality of the processes of humour unless it can be determined that the entirety of the subjective or objective approach is invalid (which is not the case). As such, it is necessary to create subjectivist and objectivist definitions and synthesize them in order to come up with a relationist definition.

4.1.1 Subjective definition

Humour can be seen to be subjective in the sense that funniness is not a quality that exists inherently in perceivable objects or actions: specific object(s) or action(s) can never be considered to be definitively humorous (Bliss, 1915; Humphrey 2016; Hurley et al., 2011; Kozintsev, 2011). Funniness emerges as a result of cognitive processing, or to use Nicholas Humphrey's words, it is "a subjective take on an external event" (2016 p.278). Similarly, Sylvia Bliss says that science finds "in the world of thought and action nothing inherently, intrinsically comic" (1915, p.237). It is, however, possible to create humour without external input. A person can have a funny thought, idea or image in their mind, but this is also, by definition, a subjective experience. Hurley et al. (2011) put the subjective nature of humour into an evolutionary context when they stated "Humor is like redness in that it is best understood as a product of the way we have been designed by evolution to detect a certain type of information about the world" (p.17). It is possible to reconcile the misleading use of the notion of evolution as a designer, and also to gain a broader understanding of the subject, by rephrasing their statement to: humour is like redness in that it is best understood as a product of the way human cognition has, through the process of natural selection, evolved to interpret a certain type of information. To be more

specific, the cognitive processes involved in humour creation and appreciation can be seen to involve the cross-correlation of mental representations, involving perceived extrinsic information and/or purely intrinsic mental information.

Bearing in mind the preceding as well as the identified subjective elements of incongruity and emotional climate it is possible to create the following subjective definition: humour is a subjective experience involving the cognitive processing of perceived specific incongruity/incongruities concurring with a state of positive emotional valence and moderate arousal. The term “state” has replaced “climate” in relation to emotion because it removes any social implications and thus maintains the subjective aspect.

The preceding definition of humour incorporates ideas drawn from existing theories of humour, but it is proposed that there is a further element that should be added that is not present in the existing literature. Regarding the cognitive mechanics of humour, it can be seen that there is a cross-correlative cognitive process in operation; that is the essence of incongruity. It is possible for this process of cross-correlation to produce humour that is anomalous to the subjective definition that has been provided in the following way. If information (extrinsic or intrinsic) is cross-correlated with intrinsic information (i.e. memory) and in so doing is associated with previous humorous/smiling/laughter experience(s) (in relation to episodes or elements) then it has the potential to produce a humorous response with no surprise or incongruity involved. Within the subjective definition as is, a humorous episode would potentially only be funny the first time it was experienced, after that point it would cease to break a pattern of expectation because it would be held in memory: there is no surprise when you already know the punch line. It can be seen, however, that humour can be effectively repeated and repetition itself has been observed to be an effective comic tool (e.g. Double, 1991; Korczinski, 2011; Molineux, 2014; Rutter, 2001; Ziegler, 1998). One example of humorous recall that occurs in standup and other forms of comedy performance is the call-back (or reincorporation)(Chauvin, 2017; Double, 2014), where words or phrases in a performance are brought back and repeated with comic effect. The comedian will sometimes even insert a brief pause before using the callback, in order to telegraph to the audience that the callback is coming, so the audience is expecting it, and this can make it even more effective. This comic device, in conjunction with mass media exposure also has the potential to create the catch phrase (e.g. the Two Ronnies “so it’s good

night from me…and it's good night from him"; Jerry Seinfeld "not that there's anything wrong with that"[19]). While humorous effect in such instances may be partly attributable to contextual factors there remains the simple fact that it is possible to laugh at the same joke twice, which means that humour can be created without incongruity. While it may appear self-evident that previous experiences involving humour/laughter/smiling should play a role in creating humorous events this is not an aspect that I have found specifically defined in the existing literature.

The dynamic whereby humour is created by cognitive cross-correlation with memories involving humour/smiling/laughter or strictly from recall will be referred to as "humorous recall". Humorous recall is remarkable because it is predicated upon sameness while incongruity based humour is based upon difference. So we can see that humour can be stimulated by the difference(s) detected in incongruities and/or by the sameness detected in relation to humour, laughter or smiling concepts and memories, which is cognitively significant in that it means that humour can involve the processing of the characteristics of both sameness and difference.

As humorous recall is a new contribution to knowledge it is appropriate to provide a further, more practical illustration of it. Consider the following scenario, bearing in mind that its descriptive style employs humour as an illustrative and pedagogical tool[20]. Two friends, Emi and Abdul Wahid, are attending a painfully un-engaging social event due to work related obligations and their lack of courage in the face of them. They are in a generic hotel conference room dominated by round tables and beigeness, drinking lukewarm tea (the event is alcohol free) while Chris de Burgh's "The Lady in Red" languishes in the background. The room is filled with military personnel in uniform, the mood is formal and stolid, and Emi and Abdul Wahid are finding that despite their best intentions they are rolling their inner eyes and succumbing to the numbing blandness. Without warning, Abdul Wahid, who has his back to the crowd, starts miming to the lyrics of "The Lady in Red" with dramatic sensual facial expressions, fluttering

[19] The Two Ronnies was a British comedy television show that ran from 1971-1987 and Jerry Seinfeld is an American comedian who has been active from 1976 until the present.

[20] The description that follows is comic and intended to briefly illustrate the pedagogical potential of humour, but it is acknowledged that "the use of humour in science communication implies risks, thus creating the possibility of polarizing the opinions of readers" (Pinto & Riesch, 2017 p.11).

eyelashes and more than a little tongue. Emi, who has been caught with a half a mouthful of Tetley's, spits the feeble brew out in a spray on the carpet where it lands with appropriate beigeness. Numerous heads in the room turn, and an elderly man, whose uniform is particularly well festooned with heroic ornaments, glares at the pair with general disapproval. Now Abdul Wahid is laughing like a naughty schoolboy and the simultaneously horrified and amused Emi ushers him apologetically from the room into the foyer and then to the street where they laugh themselves breathless and then attempt to regain their composure while a pallid man in a deflated suit lippily smokes his cigarette and eyes them with curious disapproval. From this moment on, the song "The Lady in Red", for Emi and Abdul Wahid, has become funny in and of itself. Regardless of the situation they are in, if ever either of them hears it, a broad smile stretches across their face and reflexive, unquellable laughter bubbles or bursts forth. If they happen to be together when they hear it, they inevitably both disintegrate into hysterics. If they heard it at a Chris de Burgh concert, where it would be expected and utterly congruous, it would be hysterically funny: wherever and they hear it, Emi and Abdul Rahid are experiencing humorous recall.

While it is reasonable to argue that the dynamics of memory recall in humour are characteristic of the operation of human memory in a more general sense, this issue does not affect its relevance to the subject at hand. What is important is the assertion that such dynamics should be considered to have the potential to occur within the operation of humour. As such, it is possible to incorporate humorous recall into the previous subjective definition of humour by creating the following modified version: humour is a subjective experience which, in concurrence with a state of positive emotional valence and moderate arousal, involves the cognitive processing of perceived specific incongruity/incongruities and/or correlation with memories/conceptions associated with humour, and/or smiling and/or laughter related to previous humorous experience(s).

4.1.2 Objective Definition

The arguments for the subjective nature of humour that have been presented offer little ground to present counter-arguments for objective aspects but it is possible to argue that humour can be considered to be objective by considering it in relation to complex psychological, cognitive and ecological systems. This approach can be seen in the quest to develop humour algorithms and other systems of humour generation (for reviews see Barbieri & Saggion, 2014; Mulder &

Nijholt, 2002; Strappavara et al., 2011), which would, necessarily, be inherently objective (Gillespie, 2014; Hillis at al., 2012). The development of such technology is however, still in its infancy, and the difficulty in creating such systems can also be seen as the result of trying to objectify a subjective experience.

Accepting that humour is completely subjective in nature is, however, problematic in that humour is predominantly social (Hertzler, 1970; Provine & Fischer, 1989), and as such, it extends past the subjective experience of the individual. This is well summed up by Hardin and Higgins:

> in the absence of social verification, experience is transitory, random, and ephemeral / once acknowledged by others and shared in a continuing process of social verification termed 'shared reality', experience is no longer mere capricious subjectivity, but instead achieves the phenomenological status of objective reality (1996 p.1).

Consideration of social aspects brings us back to the notion of humour being divided up into the process of its creation/expression and the process of its perception/appreciation, though it also possible that humour could be perceived in the external environment by more than one person and be thus objectified without the need for creation/expression. In this way, it can be seen that the most simplistic objectifying factor is that of smiling/laughter responses.

The relationship between laughter and humour is a complicated one, but for the purposes of providing a loose definition of humour to apply to the evolutionary framework in question, it is appropriate to make the positive correlation between humour and smiling/laughter as per Vaid and Ramachandran's assertion that laughter is an "overt behavioural marker of humour" (2001 p.426). Before applying smiling and laughter to a definition of humour, it is necessary to clarify that the relevant types of laughter and smiling relate only to "normal" (i.e. non-pathological) laughter and smiling, and not to the laughter and smiling that result from pathological conditions such as Angelmann syndrome and gelastic epilepsy (for an overview of pathological laughter and smiling see Black, 1982; Wild et al., 2003). Also, the relevant types of laughter and smiling are limited to reflexive or Duchenne examples. The term "Duchenne" is derived from Guillaume-Benjamin-Amand Duchenne, a pioneer in the field of neurology who was interested in the idea that the expressions of the human face are a gateway to the soul of man (1990). Duchenne (or "real") smiling and laughter is reflexive and involves the raising of the lips, utilizing the

zygomaticus major and zygomaticus minor muscles and it causes crow's feet around the eyes by employing the orbicularis oculi muscles. Non-Duchenne (or “fake”) smiling and laughter is voluntary and involves retracting the angle of the mouth using the risorius muscles producing a smile that does not involve the skin around the eyes. The voluntary nature of non-Duchenne smiling and laughter makes it both more neurologically and behaviourally complex, and the laughter and smiling that is used as an integrative part of communication in the absence of humour is typically non-Duchenne in nature (eg: Gunnary & Hall, 2014; Hecht & LaFrance, 1998; Mehu, 2011; Provine, 2016). In contrast, the reflexive nature of Duchenne smiling/laughter can be seen to ensure a more specific and direct correlation with humour.

Finally, it should also be recognized that the stimulus for humour, whether intrinsic or extrinsic, conceptual or perceptual, accidental or intentional, must be considered to be part of the process of humour and incorporated into any definition of humour. Due to the significance of subjectivity in the defining of humour, a separate objective definition will not be provided; instead, the objective aspects that have been discussed will be incorporated in order to create a relationist definition. Consideration of all the preceding yields the following definition:

> humour is a primarily subjective experience which, in concurrence with a climate of positive emotional valence and moderate arousal, involves the cognitive processing of perceived specific incongruity/incongruities and/or correlation with memories/conceptions associated with humour, and/or smiling and/or laughter related to previous humorous experience(s), typically causing reflexive (Duchenne) laughter and/or smiling, as well as the specific intrinsic or extrinsic input that triggers this process.

The preceding definition is appropriate for the task at hand and incorporates the notion of humorous recall, which is an important novel concept in the defining of humour. Using this definition it is possible to continue examination of humour in an evolutionary context which will begin with the consideration of the homology of relevant factors in order to get a clearer understanding of the subject and determine the veracity of the homologous approach that has been discussed.

5 Background Phylogeny

In order to understand the emergence of humour it is necessary to determine whether the laughter and smiling[21] that occurs in humans represent homologues (are inherited from a common ancestor) or are merely analogous (shared as a result of convergent evolution). For the purposes of clarity and simplicity I will, in agreement with Provine (2001), simply use parenthesis when referring to smiling or laughter in relation to animals rather than resort to terms like "vocal play-face" (Caron, 2002, p.31). It is reasonable to begin consideration of the emergence of humour with laughter and smiling because they represent specific definable biological mechanisms that can be seen to have emerged before humour itself. As Kozintsev stated, "(l)aughter occupies a peculiar place on the interface between biology and culture. While its cultural aspect arouses the greatest interest its original function must be sought in the precultural past." (2011 p.80). It has been noted by many scholars that laughter and smiling can be stimulated by means other than humour (e.g. Hurley et al., 2011; Martin, 2010) and this raises the question: is it possible for there to have been a homologous progression of stimuli leading to humour during the course of hominin evolution?

5.1 Smiling and laughter in non-human animals

As was just mentioned, while laughter and smiling can indicate the presence of humour, they do not guarantee it and this distinction is well expressed by McGhee: "smiling, laughter, and play must be ruled out as indices of humor in animals" (1979 p.87). The conflation of laughter and humour should be avoided as it can lead to errors in logic and resulting understanding of the subject: humour involves a type of stimulus and smiling and laughter are types of responses[22]. Many researchers have failed to avoid this error. For example, Wild et al.'s assertion "laughter and humour have been constituents of humanity for thousands if not millions of years" (2003, p.2121), and Scruton and Jones' paper "Laughter", which begins:

> (m)an is the only animal that laughs but it seems that laughter belongs also to the immortals. A starting point for all enquiries into laughter must therefore be the hypothesis that it is an attribute of reason (which is the quality that distinguishes men and gods from

[21] From this point on, laughter and smiling is assumed to be reflexive (Duchenne) unless otherwise noted.
[22] It is reasonable to include responses when considering humour in general terms but the stimulus and response should not be conflated.

> animals). That gets us no further than our definition of reason. If all we can say is that reason is the feature which distinguishes men and gods from the humourless animals, then it gets us nowhere (1982, p.197).

Scruton and Jones have not only made the error of conflating laughter with humour but have coupled it with the claim that animals do not laugh, and whether or not other animals smile or laugh has been the subject of much study, conjecture and dispute. The typical view on the subject until the mid-twentieth century is well expressed by Addison's assertion "Man is distinguished from all other creatures by the faculty of laughter'' (1712, p.1). Milner coined the term "homo ridens" (Latin for "laughing man") to define the human species (1972), and similar views have been put forward by many scholars (e.g. Apte, 1985; Bliss, 1915). In the later 20th century, there was a shift in ideas toward the other end of the spectrum witnessed in various research projects on "laughing" and "smiling" in apes (e.g. Gardner & Gardner, 1989; Ross, Owren, & Zimmerman, 2009), monkeys (e.g. Preuschoft, 1992), rats (e.g. Panksepp, Burdorf, 2003; Rygula, Pluta & Popik, 2012) and dogs (e.g. Fox, 1974; Simonet, Murphy & Lance, 2001; Simonet, P., Versteeg, D. and Storie, D., 2005).

Establishing a credible homology for human smiling and laughter from "smiling" and "laughter" in animals such as dogs and rats is problematic because of the very early dates of divergence (dogs: 96 MYA (Million Years Ago)(Hedges et al., 2015); rats: 90 MYA (Hedges et al., 2015)). Regarding rats, Panksepp and Burgdorf (2003) speculate on the possibility of such a homology but ultimately remain cautious: "Whether these are homologous vocalizations, and to what extent there are ancestral relations to human laughter awaits a more comprehensive neural and genetic understanding of the underpinnings of this behavior than presently exists" (p.537). In the case of dogs there is the additional complication of domesticity. Estimates as to how long dogs have been domesticated vary from approximately 16,000 YBP (Years Before Present)(Pang et al., 2009) to 100,000 YBP (Vila et al., 1997) but in either case the behaviors in question must be considered to be the product of extensive interaction with hominins though, admittedly, it does not appear that there are any laughter/smiling studies of their direct ancestor the wolf that can confirm this.

Searching for a homologous path between laughter and smiling in humans and other animals is more easily done in relation to apes (and to a lesser extent, monkeys), and this has been done in some detail (e.g. Gardner & Gardner, 1989; Goodall, 1986; Preuschoft, 1992; Ross, Owren, &

Zimmerman, 2009; van Hooff & Preuschoft, 2003). There remains some debate as to whether "laughter" in higher apes should be considered to be true laughter (i.e. whether it is substantially similar to human laughter in its forms and functions) as is evidenced by such vocalizations being described as "remotely akin to laughter" (Kohler, 2013 p.307) or "somewhat analogous to laughter" (Yerkes and Yerkes, 1932 p.159) and only demonstrating "a rudimentary relation to the human laughter" (Kellogg & Kellogg, 1933, p.169). One of the primary differences between the mechanics of human laughter and that of great apes is that human laughter, much like speech, is produced exclusively during exhalation (egressive) while ape "laughter" typically involves both inhalation (ingressive) and exhalation (Ross, Owren, & Zimmerman, 2010). The Ross, Owren, and Zimmerman paper states "(a)irflow results showed that all great apes produced both consecutive egressive calls (during exhalation phases) as well as alternating egressive-ingressive sounds (during exhalation-inhalation phases), with the latter being predominant in chimpanzees…(i)n contrast, humans emitted exclusively egressive laughter." (2010, p.1106).

Provine has hypothesized that the exclusively egressive laughter that exists in humans is connected with bipedality in human ancestors and has claimed that this "freed the thorax of its support role in quadrupedal locomotion, a critical step in uncoupling breathing from running, providing humans with the flexible breath control necessary for speech and our characteristic laugh" (2004 p.215), which indicates a possible link between laughter and speech.

The egressive/ingressive dynamic in combination with other differences in physiological/mechanical aspects involved provides reasons why the sounds that are produced in ape "laughter" are so different from the sounds of human laughter. Provine describes how recordings of ape "laughter" were not recognizable as laughter to college students, with only two students in a sample group of 119 being able to identify the sound as laughter. The sound of ape "laughter" was most commonly perceived by the group as panting or indicative of a respiratory ailment (Provine, 2001). It is notable that the study eliminated the visual and situational elements and simply isolated the sound itself. When ape "laughter" is seen as well as heard it is more easily identifiable because despite the sonic differences from human laughter, the visual and situational elements communicate a great deal of information. The visual connection between ape and human smiling and laughter responses is well illustrated by a series of photographs that Nadezhda Ladygina-Kohts used to compare the "laughter" and "smiling" of a chimpanzee named Joni with the laughter and smiling of her own son Roody

(taken from Leavens, 2009).

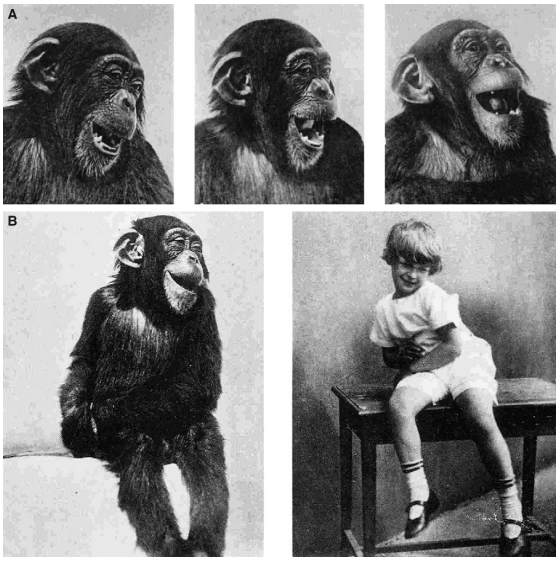

Figure 2:
Visual similarities in smiling/laughter between humans and apes. (Leavens, 2009[1])

The preceding photographs and the observations of the numerous researchers previously mentioned suggest that apes can exhibit behaviours that bear a strong resemblance to human smiling and laughter, but does this indicate a possible homologous progression? The prevailing opinion is that this is indeed the case: “Human laughter is evolutionarily grounded: laughter has evolved in each extant ape lineage from a related acoustic response exhibited by the last common ancestor of humans and apes” (Leavens, 2009 p.R511). Caron concurs with this, stating that laughter and smiling “appear to have a phylogenic origin and thus are always present in any human culture” (2006 p.255), and a similar view is given by Provine (2004). Ross, Owren and Zimmerman sum up the issue by saying there is “strong evidence that tickling-induced laughter is homologous in great apes and humans and support the more general postulation of phylogenic continuity from nonhuman displays to human emotional expressions” (2010 p.1106). They go on to propose that laughter first appeared between 10 and 16 MYA and was produced by the last common ancestor of apes and humans (2010).

5.2 Smiling and laughter phylogeny

To this point laughter and smiling have been considered as a single category, which is in agreement with the observation that smiling necessarily co-occurs with laughter (Pollio, Mers and Lucchesi, 1972), but some consideration should be given to the possibility of a convergent

evolutionary path. It has been asserted that laughter and smiling in humans can be seen to have a phylogenic origin that goes back at least as far as the last common ancestor of humans and apes but there are also crucial differences between the related behaviours that can be observed in humans and animals. Van Hooff (1972) has proposed that smiling and laughter have different phylogenic roots: smiling derives from a silent bare-teeth display that is associated with submission (e.g. De Waal and Luttrell, 1985), and laughter from a relaxed open-mouth "play face" that is associated with positive emotional valence (Matsumoto et al., 2008; Van Hooff, 1972). This has subsequently been supported by further research (e.g. Burrows et al., 2006; Preuschoft, 1992) and the view that these two displays have converged during the course of evolution within prosocial and affilliative contexts to become Duchenne smiling and laughter has become widely accepted (e.g. Davila-Ross et al., 2015; Preuschoft and Beckmann, 1995; Preuschoft and van Hooff, 1995).

What still remains, however, is the question of how this convergence may have come about? One possible solution lies in Van Hooff and Preuschoft's (1995) "Power Assymetry" hypothesis which Dunbar and Mehu summarize as follows:

> (u)nder conditions of hierarchical and strongly asymmetrical relationships between individuals, distinct displays of submission and appeasement, of affiliation, and of playfulness will be present, whereas in egalitarian relationships the displays of submission and affiliation, and those of appeasement and playfulness will converge (2008 p.272).

Dunbar and Mehu's testing of this idea yielded mixed results however, which begs the possibility of another explanation. It is proposed that the explanation is alluded to in Van Hooff's acknowledgement of a causal relationship between laughter and smiling: "the baring of the teeth may also be seen as a secondary effect of the vocalization reflex, the muscles of the mouth and throat region being tensed during strong vocalization in order to protect the vibrating tissue" (1972 p.214). This is confirmed by the observation "laughter always gradually fades out as a "smile" and may also be preceded by it" (Pollio, Mers and Lucchesi, 1972). The role of smiling preceding laughter is noted by Haakana who stated "Smiling can be used as a pre-laughing device: laughing together can be entered step-wise, and smiling is a common device for paving the way to the laughter" (2010 p.1499). In personal communications with Willibald Ruch, he expressed in an e-mail that it is physiologically impossible to laugh without smiling. In support of this view he cited the following video evidence which shows people attempting to laugh without

smiling: https://www.youtube.com/watch?v=7KqgWfut6Ic (Ruch, W., 2016, personal communication, December 18th). This relationship between laughter and smiling is also reflected in the French word for smile, "sourire", which can be roughly translated as "sub-laugh".

Bearing this in mind, the emergence of laughter would have necessarily yielded a reflexive Duchenne bare-teeth display (ie**:** smiling), with a different causal mechanism in comparison to the previously existing silent bare-teeth display. This means there would have been an analagous display reflexively produced by the physiological dynamics of laughter, producing a single facial display with the potential to represent two distinct messages. Laughter necessarily yielded smiling, and so, if laughter became a more prevalent behaviour due to superior adaptive benefits or other reasons, it would have resulted in a higher liklihood of convergence: an unambiguous signal is more efficient than an ambiguous one. In this scenario, the semiotic aspects of the silent bare-teeth display would have become secondary and research indicates that they are more prevalent in non-Duchenne smiling, which is primarily used as a deceptive signal to mask feelings and a method of communicating appeasement but can also signal positive emotion (Bonanno et al., 2002; Ekman, Friesen, & O'Sullivan, 1988; Fridlund, 1991; Hecht & LaFrance, 1998; Keltner, 1995; Prkachin & Silverman, 2002).

In sum, based on the preceding, it is reasonable to believe that during the course of evolution the communicative dynamics of smiling came to combine those of the precedent bare-teeth display and those of the reflexive display resulting from the physiological constraints of laughter. The "power-assymetry" dynamic was merely a possible element in a more complex process that primarily hinged on the question of which of the two behaviours was of the greatest adaptive value. The result of this process was the modern human smile (Duchenne and non-Duchenne). In evolutionary terms it is possible this might have resulted in the convergence of emotional/behavioural aspects of the silent bared-teeth display in the mechanics of humour itself.

By affirming the role of laughter in Duchenne smiling it is possible to see laughter and smiling as existing on a continuum, as has been proposed by many researchers including Ekman and Friesen (1982) and Owren & Bacherowski (2001). Within this continuum it will be assumed that in a general sense "laughing occurs at higher levels of exhiliration, and smiling is typical of lower levels " (Ruch, 1993 p. 608). Kuhn has provided a breakdown of 15 different levels within this spectrum: smirk, smile, grin, snicker, giggle, chuckle, chortle, laugh, cackle, guffaw, howl, shriek, roar, convulse, and die laughing (1994). The continuum approach of smiling and laughter

corresponds with observations I have made both in performing and teaching comedy. Related to this, one of the biggest misconceptions that aspiring comedians have is the belief that the specific purpose of stand-up is "to make people laugh" and that laughter is the only criteria by which they should measure their success. Laughter is, of course, typically a desirable response for a comedian, but an audience can enjoy and be amused by an aspect of the performance without having to actually laugh, and recognition of this dynamic by the comedian is valuable in helping them create and deliver their material (Molineux, 2014; Ruch, 1995).

5.2.1 Duchenne laughter and smiling

As was previously mentioned, smiling and laughter can be considered to fall into two categories: Duchenne (reflexive) and non-Duchenne (voluntary). In evolutionary terms, reflexive Duchenne responses can be seen as a more ancient form and non-Duchenne use would have emerged later because it was necessarily more neurologically complex due to the involvement of voluntary control. This is evidenced by the fact that only a few more cognitively advanced species are capable of the non-Duchenne (Diogo & Wood, 2011). Reflexive smiling/laughter are activated by different cortical regions than similar voluntary smiling/laughter (e.g. Iwase et al., 2002) and there is evidence of the more recent origins of non-Duchenne expressions in the phylogeny of related musculature: non-Duchenne laughter involves the risorius muscle, and the only animals other than humans that appear to have a distinct risorius muscle are chimpanzees and gorillas[23] (Diogo & Wood, 2011). Davila-Ross et al. (2011) have said that research to determine whether or not apes utilize non-Duchenne smiling/laughter spectrum displays has yet to be conducted, but the documented ability of chimpanzees to produce laugh-elicited laughter (i.e. contagious) that differs in acoustic form from their spontaneous laughter suggests that this is likely to be the case. The fact that the risorius muscle is only evident in the most cognitively advanced higher apes is also indicative of a specific correlation between cognitive development and the use of laughter as a communicative signal, and the emergence of the non-Duchenne may have been the result of the “ritualization” process discussed by Van Hooff (1972).

[23] This is further evidence that the silent bare teeth display is subordinate.

In relation to the origins of language, the emergence of non-Duchenne smiling and laughter was significant because it created a connection between laughter/smiling and voluntary communication. Both messages, that of submission communicated by the silent bare-teeth display and that of positive emotion communicated by laughter and related smiling, would have, in different ways, helped to facilitate positive social interactions and encouraged face to face communication. As such, smiling would have served as a social bonding mechanism with the potential to induce positive affect in others (as per Owren & Bachorowski, 2003). More generally, the development of voluntary smiling and laughter was a significant evolutionary progression restricted to only the most cognitively advanced species. This level of progress occupies a middle ground between the reflexive "smiling" and "laughter" displays present in a range of monkeys and apes, and humour, which is present only in humans. It is also notable that voluntary smiling and laughter are to some degree, inherently deceptive. I have not been able to find any research documenting the use of voluntary smiling and/or laughter as a form of tactical deception in apes, as is the case with humans (Lewis, Stanger, & Sullivan, 1989; Ekman et al., 1991), and the capacity for this type of behaviour may be seen as another possible progressive step that occurred prior to the emergence of humorous behaviour.

The preceding provides the requisite understanding of smiling and laughter required for an examination of humour in an evolutionary context. It should be noted that smiling and laughter are primarily considered to exist on a spectrum, but the evolutionary role of the silent-bared teeth display is acknowledged and may have sown the seeds for aspects of aggression that exist in humour.

5.3 Phylogeny and Ontogeny

Before moving on to discuss a possible homologous evolutionary path for the different forms of smiling and laughter stimuli it is first necessary to consider the potential value of correlating ontogenically[24] based observations and theories with phylogenic ones. In general terms the notion of ontogeny recapitulating phylogeny is a discredited one; human fetuses with gill slits are tiny not fish replicas of their water-breathing ancestors. This, however, is a very generalized

[24] The term "ontogeny" refers to the process of human development from the in-utero phase until maturity.

perspective and Gibson notes that “ontogenic prospectives have become the rule, rather than the exception, among serious scholars of cognitive and linguistic evolution” (1994 p.274) and this opinion is supported by many others (e.g. Fuster, 2002; Bickerton, 1990; Foster, 1994, Givon, 1998). Despite the substantial level of endorsement that exists within academia for an ontogenic/phylogenic parallels approach, there remain some concerns (for a review see Slobin, 2004), and central among these concerns is the following, pointed out by Jespersen (1923) and summed up by Slobin: “(t)he Homo sapiens child is different from a pre-human hominid in two critically important ways. The child is exposed to some already evolved human language and is equipped with a brain that evolved to make use of such a language.” (2004 p.255). This statement is as applicable to humour as it is to language, and will be taken into consideration. It is also important to note that it is not proposed that ontogeny strictly recapitulates phylogeny, but instead that it represents a general indicator of possible developmental parallels as Piaget proposed in his book “Behaviour and Evolution” (2013).

In terms of basic relevant ontogenic data, babies smile spontaneously in utero (Campbell, 2004) and as new-borns (Wolff, 1959; Kawakami et al., 2006), with “a large increase in smiles after 10 days and, possibly, another increase after 51 days” (Kawakami et al., 2006 p.65). Spontaneous laughter is one of the first social vocalizations (Deacon, 1997). It occurs as early as 17 days (Kawakami et al., 2006) and its slightly later appearance is most likely due to the more advanced physiological aspects of laughter in comparison with smiling. Smiling and laughter can also be considered to be innate because they can be observed in children who are blind and deaf at birth and so cannot be learned behaviours (Van Vugt et al., 2014). In phylogenic terms, Panksepp and Bergdorf claim that the ontogenic timetable related to laughter and smiling “suggests an ancient heritage” (2003 p.541).

Moving further along this timetable, it can be seen that within five weeks smiling and laughter are no longer merely spontaneous but can be caused by external stimulation as is shown in Mireault et al.’s summary of Wolff’s timetable of humour development, which runs as follows: “social smiling (5–9 weeks)… followed by laughter in response to physical stimulation (3 months), social games (5 months), and visual events (7–9 months), and finally humor creation (9–11 months) and “clowning” (i.e. creating absurd events; 10 months)” (2012 p.798). In comparison to this timetable, language emerges at a later phase of ontological development: “infants smile and laugh months before they babble, gesture or speak” (Mireault et al., 2012 p.339), but more significantly, infants can create humour before they can speak (9–11 months), and do so in the same phase when babbling occurs. Babies first produce their proto-imperative

vocalizations (i.e. babbling) between 7 and 10 months (Pettito & Marentette, 1991). Babbling serves as a "mechanism by which infants discover the map between the structure of language and the means for producing this structure" (Pettito & Marentette, 1991 p.1495) and this yields simple aspects of speech between 12 and 18 months (Karasou & Lopez-Ornat 2013; Macneilage & Davis, 2000). Research supports the more general notion that humour precedes language in infant development; parents tend not to look at their 5 month old child and think, "I can't wait until they can speak so we can get past this bleak, humourless stage". This hierarchy is also evident when taking into account the fact that humour can result merely from perception/cognition: it does not require creation. In contrast language requires a mutually understood code of symbolic reference, the voluntary expression of symbolic thought in a syntactic format, and development of relevant complex motor skills for even the simplest expressions.

To summarize, in ontogenic terms, humour can be seen to emerge at an early stage suggesting an ancient phylogenic heritage. Humour perception and creation precede language in ontogenic development and, as was already discussed, it is reasonable to draw parallels with phylogenic development. Bearing this in mind it is worth noting other ontogenic observations that imply that elements of humour serve as cognitive building blocks in the progression towards language competency. These include Srofe and Waters remarking on the "tendency of the infant to move toward incongruity and to find pleasure in challenges to his cognitive capacity" (1976 p.185) and Meltzoff's (1985, 1990) assertion that before full language acquisition has taken place in infancy, mutual imitation [25] between two partners serves as a principal mechanism for interpersonal communication. Humour is social, communicative, involves the cognitive cross-correlation of information and can utilize vocalizations. As such, it can be seen that mapping out a possible path of hierarchical evolutionary development of cognitive, communicative, and social aspects of humour and any related psychological and physiological components would be valuable in understanding more about the origins of language.

The preceding section serves to show the validity of examining parallels between ontogeny and phylogeny, which opens up a wealth of evidence-based research that can be applied to the subject at hand. Having established this, it is now possible to move on to examine the possible

[25] Imitation's role as a comic device discussed later in this thesis (e.g. pp.82-83)

specific causal sequences in the evolution of potential precursors to humour, and consideration of smiling/laughter stimuli serves as a good starting point for this line of inquiry.

6 Hierarchy of stimuli that elicit smiling/laughter spectrum responses

Duchenne laughter and smiling can be traced to the last ancestor common to humans and higher apes (Ross et al., 2009), but they are merely reflexive responses to stimuli and in order to understand them in terms of an evolutionary progression it is necessary to consider the different forms of stimuli that produce them. These stimuli can be divided up into three general categories: tickling, play, and humour (Gervais & Wilson, 2005; Owren & Bacherowski, 2001). The category "play", however, is broad and will be refined for the purposes of analysis. In hierarchical terms tickling is the most simplistic form of stimulus, involving physical cause and effect. Smiling and laughter stimulated by "play" transcends the specific physical causality of tickling, but it still lacks the cognitive component outlined in the description of humour i.e. there is no requirement for perceived incongruity or cross-correlation of information and if such does occur it is purely incidental. As such, the stimulus involved is more general and is associated with situational aspects relating to positive emotion and higher levels of arousal rather than to specific actions/events. Because the term "play" is more indicative of a situation than a specific type of stimulus, the term "social arousal during play" will be used instead.

The dynamics of these categories will be discussed in more detail shortly, but put simply, tickling involves specific cause and effect physical stimulus, social arousal during play involves general affective/arousal based stimulus without the necessity for physical contact, and humour involves cognitive stimulus mediated by affect and arousal as per the definition that has already been outlined. The order that these categories are listed in is indicative of their hierarchical order and is agreement with the hierarchy proposed by Karasev (1996), which drew on ideas first proposed by Beattie (1776) defining laughter as either "animal" (caused by tickling and joy) or "sentimental" (caused by ideas) (as cited in Kozintsev, 2011) and this view was also endorsed by Kozintsev (2011).

The question at hand is whether or not it is reasonable to believe that this hierarchy represents a homologous evolutionary path. Speculation on a possible connection between tickling and

humour has been going on since the earliest days of evolutionary theory, though this has sometimes manifested itself as mere analogy as in Darwin's statement: "The imagination is sometimes said to be tickled by a ludicrous idea; and this so-called tickling of the mind is curiously analogous with that of the body" (1965 p.199). Darwin, however, went on to outline a theory that tickling and humour share a common underlying mechanism, a belief that was also shared by Hecker (1873) and has come to be referred to as the Darwin/Hecker hypothesis. Support for this hypothesis has been given more recently in research based on self-reporting (Fridlund & Loftis, 1990) and on behavioral measures (Harris & Christenfeld, 1997). It shows that people more prone to laughter stimulated by tickling are also more likely to laugh at humorous stimuli. In addition to this research Willman noted that both tickling and humour involve an element of ambivalence (1940) and Suslov has proposed a cognitively based homology that relates to incongruity theory:

> The laughter from tickling can be connected with the attempt of the brain to localize the place of irritation of skin; the result of such localization is invariably rejected because the irritated place is changed unpredictably (that is the reason why the tickling should be done by another person) (1992 p.3).

Also of interest is the observation that "subjects will respond to a gesture that signals the onset of a tickle in the same way as to a tickle" (Newman et al., 1993 p.782), which is confirmed by Hoshikawa's research (1991). This implies a possible evolutionary scenario wherein smiling/laughter stimulus could have transitioned from the physiological to the cognitive/perceptual. The feasibility of this proposition will now be considered by way of a more detailed examination of the three categories that have been outlined: tickling, social arousal during play, and humour.

6.1 Tickling

It has been asserted that a homologous evolution of laughter (and laughter derived smiling) can be traced back to between 10 and 16 MYA to a common ancestor of apes and humans, and that tickling is the most simplistic form of stimulus that elicits smiling/laughter spectrum responses. Tickling can be divided into two types as per Hall and Allin (1897): knismesis and gargelesis. Knismesis is "an aversive, annoying sensation from light movement across the skin,

akin to a crawling insect" (Seldon, 2004 p.93) and while attribution of this sensation to unicellular organisms (Stanley, 1898) might be a little far reaching, knismesis can be seen in a wide variety of animals and as such, necessarily has an ancient evolutionary origin. Knismesis is caused by low-level stimulation of sensitive areas of the body, typically by small moving objects such as insects or parasites. In behavioural terms knismesis usually triggers some type of reaction to remove the irritant. This can be seen in horses, cows, and other animals when they twitch their skin and brush the area with their tails, and the human experience of knismesis could be characterised as an alarming itch. Knismesis does not result in laughter (Harris, 2012) but there is some correlation in that it can cause reflexive reactions involving rhythmic muscular contractions. There is an evident adaptive value to knismesis as it helps in the detection of organisms that could cause stings, infestations, disease or other deleterious effects (Seldon, 2004).

Gargelesis is "a pleasurable feeling from a rougher, deeper pressure, stroked across the skin in certain regions." (Seldon, 2004 p.93) and is innate in humans (Scheiner et al., 2006). Gargelesis can stimulate smiling and laughter, and, as was previously mentioned, this has also been observed in a variety of animals including rats (e.g. Panksepp, Burdorf, 2003; Rygula, Pluta & Popik, 2012), dogs (e.g. Fox, 1974; Simonet, Murphy & Lance, 2001; Simonet, P., Versteeg, D. and Storie, D., 2005) and non-human primates (e.g. Gardner & Gardner, 1989; Ross, Owren, & Zimmerman, 2009). The ticklish areas of apes are much the same as humans: feet, armpits, stomach and sides (Provine, 2001). Unlike humans, however, apes are able to tickle themselves (Kellogg & Kellogg, 1933; Goodall, 1986). The ability to self-tickle suggests a lower level of cognitive processing that does not involve a forward model that predicts sensory consequences of self-produced tactile stimulation followed by the attenuation of the sensory effects of that movement as per Blakemore, Wolpert and Frith's model (2000). This implies that following the break from the last common ancestor of apes and humans, hominins experienced increased activity within, and associated development of, neurological structures related to such a model[26].

[26] It may eventually be possible to date this transition by determining related genetic markers and correlating these with analysis of genetic material in hominin remains.

In physiological terms, research comparing the acoustical properties of tickle induced laughter in humans and great apes have shown that human laughter differs in that it is primarily egressive and involves more vocalization, which utilizes consistently regular vocal-fold vibration (Ross, Owren, & Zimmerman, 2009). These mechanics and their related physiology are also required in speech, and Ross, Owren and Zimmerman cite this as being "potentially significant for language evolution" (2009 p.1107). Another connection between laughter and language can be seen in Wattendorf et al.'s research, which has shown that ticklish laughter in humans activates the supplementary motor area of the brain that is associated with song production and speech (2012). They state "(t)ickling and laughter is also associated with specific activities in higher-order sensory-motor areas (SII (secondary somatosensory areas) and the cerebellum), possibly paving the way to the deliberate control of the ensuing vocalization". I was not able to find any similar studies in apes to contrast this with. In relation to ontogeny/phylogeny, there is a possible parallel in the fact that instances of ingressive sounds are much more likely to be produced in the laughter of young children than in the laughter of adults (Ross, Owren, & Zimmerman, 2009 p 1008).

At a general level, the most distinctive feature of tickling as a form of smiling and laughter stimulus is the fact that it involves direct physical cause and effect, which differentiates it from the other two forms of stimuli. Kozintsev has argued that there is also a degree of mediation by "interpersonal" factors such as mood (2011), though there is some clinical evidence to the contrary (Leuba, 1941). Tickling is generally associated with positive mood in both apes (Gamble, 2001) and human children, and takes place in parent/infant interactions in both human and apes (Parker & Milbrath, 1994; Tomasello, 1996) as a simple way for parents to communicate with infants at a point when the infant possesses limited communication skills. Tickling is also a component of social grooming in apes (e.g. Markus & Croft, 1995; Merrick, 1977; Shimada, 2013), and in this context there are communicative elements in the action of tickling and in the audio and/or visual information yielded from the resulting smiling and laughter. In relation to social grooming Dunbar has made the assertion based on documented observation that tickling/smiling/laughter can be seen to be constituent elements in a broader communicative social bonding system (Dunbar, 1998(b)). He has extended this into what is

arguably a much less defensible theory[27] that proposes language evolved from social grooming, and within this theory tickling, smiling, and laughter would have played a role in the evolution of hominin communication (Dunbar, 1998(b)).

While tickling is a behaviour that can be seen as being distinct from play (Provine, 2001), it is during play situations that tickling most often occurs, both in humans and in apes (Gardner & Gardner, 1989; Goodall, 1986; Provine, 2001). Provine describes laughter as "the sound of play" (2004, p.216) and the play environment provides a situation involving positive emotional valence, which Kozintsev claims is a prerequisite for tickling (2011). Positive emotional valence was included as part of the definition of humour, which supports the notion of a homologous progression. In social terms, tickling occurs during juvenile-to-juvenile play in apes (Gardner & Gardner, 1989; Goodall, 1986) and as well as in mother-baby play in chimpanzees (Plooij, 1979). Plooij observed that baby chimpanzees will bite the mother to get her attention/engage her and then the mother will tickle the baby, typically to a threshold point. When the baby recovers it begins the process again by biting the mother (Plooij, 1979). This is reminiscent of Dunbar's observations on the communicative element of social grooming and is another example tickling/smiling/laughter functioning as communicative tools. It is also notable that tickling is a distinctly ambivalent stimulus and can evoke pleasure and displeasure (Plessner, 1970). As such, tickling, or the threat of it, has the potential to cause panic and anxiety. This ambivalence offers further support for the notion of a homologous progression from tickling to humour in that humour also has an ambivalent nature with affliative and aggressive elements (Berk 2001). It is possible that the ambivalent nature of tickling may have evolved to manifest itself in behavioural aspects of humour such as those outlined in Superiority Theory and be strengthened by the ambivalent nature of smiling that was discussed earlier.

In sum, there is a substantial body of evidence showing correlations between tickling and humour suggesting the possibility of a homologous evolutionary path. If this were the case, social arousal during play might have functioned as a transitional phase between the two and this possibility will now be considered.

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[27] Further consideration of this is not valuable in the context of the thesis and is not pursued due to present limitations.

6.2 Social arousal during play

Gervais and Wilson's assertion "(t)ickling in conjunction with mock aggression and chasing is the prime elicitor of ape laughter (Fry 1994; Provine 2000; Gamble 2001) as well as laughter in human infants (Sroufe and Waters 1976) and children (Harris 1999; Provine 2000)" (2005 p.398) supports the notion of a homologous progression from the stimulus of tickling to the stimulus of social arousal during play. Further support is given by the fact that the elements of ambivalence and an elevated level of arousal are both seen in social arousal during play as well as during tickling. An excellent example of the role of an elevated level of arousal in stimulating laughter in chimpanzees can be seen in chasing games (Davila-Ross et al., 2015; Provine, 1996), which can occur without any actual physical contact because the essence lies in the potential for contact rather than in contact itself. Elicitation of smiling/laughter spectrum responses during chasing games is representative of a more evolutionarily advanced form of stimulus devoid of the requirement of direct physical cause and effect involved in tickling. The threat of physical contact is sufficient in a play situation involving a positive emotional valence and elevated state of arousal.

It is worth noting the roles of arousal and homeostatic regulation in play. As has been discussed, these are aspects cited in humour theories and similiarly, Huizinga notes that play functions as a "discharge for superabundant vital energy" (1949 p.2). Relevant to this is "eustress" (a positive stress that enhances function), which can be associated with both positive emotional valance and increased arousal (Harris, 1970; Selye, 1956). Eustress has shown to be neurologically distinct (Berk et al., 2012) from "distress" in EEG metrics and Berk et al. specifically cite "eustress" as a aspect of humour (1993). The state of eustress occurs during play (Corbin, 2007), and laughter/smiling communicate the presence of a positive emotional state and can serve to prolong play (Davila-Ross et al., 2011; Waller & Dunbar, 2005) constituting a reinforcing reward dynamic[28]. Put in a broader social/behavioural context, laughter and smiling within play "promotes social affiliation and supports an interactive platform for young individuals to develop cooperative and competitive behavior" (Davila-Ross et al. 2011) and from a neurochemical perspective, play involves the release of endogenous opioids that facilitate social bonding (Launay et al., 2016; Nelson & Panksepp, 1998). So it can be seen that in social,

[28] This type of dynamic will be discussed in the "Rewards" section (see pp.68-73).

behavioural, psychological, and even neurochemical terms, play would have provided a evolutionary situation that would have facilitated the emergence of humour by way of social arousal during play.

In sum, the stimulus of social arousal during play can be thought of as a type of eustress, involving a positive emotional valence in combination with an increased level of arousal, within a play situation. Social arousal during play is present in higher apes and humans and the interrelationship between tickling and play supports the idea that it emerged homologously through tickling during play. It is, however, distinct from tickling because it does not involve specific physical cause and effect (i.e. touch). While affect and arousal are the key elements within this type of stimulus they are mediated by cognitive processes: there is cognitive processing of situational elements triggering arousal and positive emotion. The key word in the preceding sentence is situational, because it indicates that the cognitive assessment occurs in relation to multiplicitous input rather than specific input. Chasing is an excellent example of this because it occurs as a temporal sequence comprised of numerous constituent actions and it is the totality rather than the specific constituents that trigger smiling and laughter. Social arousal during play can be seen as representing an intermediate phase between tickling and humour but the key innovative element in the transition to humour would have been the development of a mechanism to elicit smiling/laughter responses from specific cognitive/perceptual events.

6.3 Humour

The stimulus of humour is distinct from the stimulus of social arousal during play because it is primarily predicated on the cognitive processing of specific information. To give this greater clarity, it is helpful to recap the definition of humour being applied:

> Humour is a primarily subjective experience which, in concurrence with a state of positive emotional valence and moderate arousal, involves the cognitive processing of perceived specific incongruity/incongruities and/or correlation with memories/conceptions associated with humour, and/or smiling and/or laughter related to previous humorous experience(s), typically causing reflexive (Duchenne) laughter and/or smiling, as well as the specific intrinsic or extrinsic input that triggers this process.

Laughter and smiling responses stimulated by social arousal during play lack the cited element of "the cognitive processing of perceived specific incongruity/incongruities"; the cognitive processing involved agglomerated information rather particulated information. Put simply, it is the difference between laughing because of a specific event/idea, and laughing because of the totality of a situation. Having reviewed the specifics of the stimulus of social arousal during play, it is reasonable to believe that a homologous progression was possible[29], and one potential path would have been a progression from stimulation by the general threat of tickling to stimulation by a specific action representative of the threat of tickling within a play situation (the preceding also involves symbolic communication). Provine offers a similar suggestion for the origin of humour: a feigned tickle (2000, p.96). A feigned tickle, however, is however, more cognitively and behaviourally complex than the scenario being suggested here because, not only does it involve creation as well as perception, it also involves feigning, which is a voluntary act involving strategic deception. In contrast, what is being proposed here is a situation where the required stimulus is determined by the mere perception of an action with no intentional requirement for the creation of the action, let alone strategic intentionality. Provine's own research supports this possibility as is shown in his observation "simply the threat to tickle can serve as a conditioned stimulus" (2000, p.125).

Within the proposed dynamic there is, however, still the need to reconcile the element of incongruity, which is a central part of the provided definition of humour, and in this regard, the importance of surprise in incongruity (Brownell et al., 1983; Shammi & Stuss, 1999; Suls, 1972) is relevant: the threat to tickle involves one individual trying to surprise another with quick unpredictable movements. As such, it involves breaks in patterns of expectation i.e. incongruity. As such, the situational aspect of surprise can always be viewed as a transitional phase that gradually evolved in humorous dynamics towards its cognitive root: incongruity. This final transition could have occurred simply through habituation. As the behaviour in question became habituated, the unpredictable movements that were involved would have become increasingly associated with smiling/laughter, and thus, potentially able to stimulate smiling/laughter (as per the notion of humorous recall) even in the absence of the threat to tickle. The resulting progression would have been roughly as follows: sharp shift in a specific spatial event → sharp

[29] There is also evidence that higher apes in captivity have the capacity to utilize incongruity in social play (Gamble, 2001).

cognitive shift re: perception of sharp shift in specific spatial event → association of laughter/smiling with sharp shifts in cognition. Further extrapolation of this is unnecessary at this point, but bearing in mind the preceding it is reasonable to now attribute a homologous evolutionary path from the stimulus of tickling to the stimulus of humour. Falks concurs with this conclusion stating "the range of stimuli for laughter expanded from the physical contact and tickle of chimpanzees to the more subtle symbolic play of humor" (2004, p.495).

Referring back to the possibility that the ambivalence of tickling may have carried through to humour it is notable that in the presented scenario the earliest forms of humour would have involved an elevated level of arousal and the potential for mock aggression. Similar dynamics have been observed in the rare examples of humour (or proto-humour) that have been observed in apes in captivity, such as the chimpanzee Washoe urinating on Roger Fouts (Miles, 1986 p.251) and then signing "funny", and the chimpanzee Styopa throwing feces at workers at the Pavlov Primatological Centre and then "laughing" and displaying an expression of "malice, slyness, curiosity, and playfulness" (Butovskaya & Kosintsev, 1996 p.716). At a more general level, teasing behaviour (throwing things at others, stealing etc.) has also been observed during play in chimpanzees in the wild and in captivity (Adang, 1986; Mendoza-Granados & Sommer, 1995) though evidence that smiling/laughter are stimulated by specific teasing acts is lacking. While the proposed homologous path seems plausible for hominin evolution it is notable that for whatever reasons, apes did not and/or could not follow this path. Provine notes the "failure of chimps to signal their production or perception of humor with laughter" (2001 p.94) and even apes in captivity that have been taught language have not been reported to initiate, sustain and proliferate humorous behaviour as is universally observed with humans. The proposed model suggests that if humour does exist at all in wild apes (most likely chimpanzees or bonobos) it should mostly likely be found in situations involving moderate arousal, a positive emotional valence, where specific actions with the potential to trigger surprise are occurring. It is also possible that proto-humour occurred within specific events involving a high degree of singularity (without multiple contributing distinct observable characteristics) that involved a high degree of arousal and a positive emotional valance (eg: sliding down a slope) and it would be valuable to assert whether or not this occurs in higher apes.

Bearing in mind the outlined homologous path of development, humour at its point of emergence would have involved a combinatory system requiring an aroused physical state (increased respiration, etc.), an elevated, positively valenced emotional state, a degree of

emotional ambivalence (due to element of threat), the situational prerequisite of play, and the cognitive/perceptual processing of incongruous input. In relation to cognition it is notable that within the proposed model humour can be seen to have originated from social interaction rather than through isolated, intrinsic cognition as is suggested by the Hurley et al. (2011) model, which characterizes social humour as a more complex ”higher order” form and asserts that the simplest form is the creation of the joke (2011). In contrast, the homologous evolutionary path that has been outlined shows the earliest forms of humour to have involved a reflexive perceptual/cognitive response to actions taking place during social interaction: humour was perceived before it was consciously conceived/created. This is the same as in ontogenic development; babies perceive things as humorous before they can create/communicate humour. In situational terms, the proposed model is in agreement with the idea that humour first occurred in situations involving play as McGhee (1979) and others (eg: Hurley et al., 2011) have suggested, and this brings up the possibility that it may have, at first, been restricted to childhood behaviour

At this point in the thesis a probable evolutionary path that led to the emergence of humorous behaviour in hominins can be seen. This makes it possible to consider the dynamics of evolutionary progress in terms of its specifics; behaviourally, psychologically, and cognitively. Before moving on to this, however, it is necessary to consider the importance of the element of neoteny that is implicit in the outlined evolutionary path.

6.4 Neoteny

Bearing in mind the idea that within the proposed model early humour was restricted to play situations, a more detailed look at the dynamics of play and the ramifications of neotenous behaviour in an evolutionary context is valuable. The play situations involved in early humour would more likely have been juvenile to juvenile rather than parent to juvenile for a number of reasons. To begin with, the type of juvenile-to-juvenile play sometimes referred to as “rough and tumble play” (eg: DiPietro, 1981; Scott & Panksepp, 2003) would have provided a more

consistently elevated physical and emotional state in all parties than parent/infant dyads[30]; and the rough and tumble aspect of juvenile to juvenile play provided the requisite element of arousal. Having reviewed the body of existing research related to arousal, Martin concludes "there is consistent support for the idea that humor is associated with increased autonomic arousal" (2010 p.62) and this is supported by the connection some scholars have made to "rough and tumble play" in regard to the ontogenic development of humour (eg: Boyd, 2004). In addition to this, children would also have been more prone to the perception of incongruity, because incongruities occur as a result of novelty in perception and during infancy and early childhood most of the child's environment is perceived to be novel, as they do not yet have sufficient experience to habituate their patterns in memory. This has been referred to as dishabituation (eg: Fantz, 1964) and it is part of the reason why children show a greater disposition to engage with novelty than adults (Fantz, 1964; Wetzel, Widman, & Schroger, 2009): in a world where everything is new, there is more novelty to engage with as well as the necessity to be open to engage with it, so that becomes the norm. So it can be seen that a dyadic parent-child interaction would have yielded a much lower overall level of perception of incongruity than a juvenile-to-juvenile play scenario involving two or more individuals. It is also notable that with juvenile to juvenile play the spread of information through social learning would have been exponentially multiplied in any play situation involving three or more people relative to that which might have occurred in a dyadic parent-child interaction. While it is not possible to rule out the possibility that humour emerged in parent-child interactions (tickling during mother-infant play is well documented in higher apes (eg: Bard, 1994; Plooij, 1979)), consideration of the preceding factors shows that it is more likely that it emerged during juvenile to juvenile play and this view has also been put forward by Martin (2010).

Based on the preceding it appears probable that humour began as a juvenile social behaviour, but what is more difficult to determine is at what evolutionary point this behaviour continued into adulthood. If early humorous behaviour was continued into adulthood, it would likely have been much less frequent due to the loss of parental security and the ecological pressures associated with survival and reproduction that would have diminished the possible frequency of social interactions with a positive emotional valence. The life of adult hominins would have centred on

[30] Parent/infant dyads involve much less rough and tumble play, particularly mother/infant dyads (Paquette et al., 2003)

the struggle to survive, and humour would have been a luxury that could only be enjoyed in youth because food and security were already provided. As such, humour would only gradually have become an element of adult hominin behaviour i.e. humour is, to some degree, neotenous. Gould defines neoteny as "(p)aedomorphosis (retention of formerly juvenile characters by adult descendants) produced by retardation of somatic development" (1977, p.483) and it has been argued that neotenous evolution has occurred in numerous human physiological characteristics that are observable in foetal and neonate apes such as hair on the head, a globular skull, ear shape, vertical plane face, and the structure of the foot (Bednarik, 2011). In behavioural terms, neoteny is most frequently apparent in domesticated animals (Price, 1984; Fox, 1978; Coppinger et al., 1987) and in humans (Gould, 1977; Brune, 2000; Gibson, 1991). While the importance of neoteny in the evolution of human behaviour has been the subject of some debate (e.g. Godfrey & Sutherland, 1996; Shea, 1989), Brune's statement "Neoteny has been considered the hallmark of human evolution, leading to persistent curiosity, playfulness, and emotional attachment" (2000 p.301) suggests a connection with humour because curiosity, playfulness, and emotional attachment are all humour-related behaviours. In the context of cognitive evolution, it has been proposed that neoteny played a positive role in the evolution of human intelligence: "the immaturity of the adult human brain permits humans to go on learning throughout their lives and accounts for high human intelligence" (Gibson & Petersen, 1991). It is also possible to link this process with Buchsbaum et al.'s assertion of a "link between the development of an extended period of immaturity in human evolution and the emergence of powerful and wide-ranging causal learning mechanisms, specifically the use of causal models and Bayesian learning" (2012). Related to this at a biological level, is the fact that there is increased brain plasticity through variation in gene expression during childhood as well as within neotenous brain structures (Goyal et al., 2014), which could have played a role in hominin evolution and is worthy of further consideration.

The hypothesis that humour is neotenous is supported by the fact that there is a greater occurrence of laughter and humour in children in comparison to adults in both humans (Provine, 2001; Martin & Kuiper, 1999) and apes (Owren and Bachorowski, 2001). There is additional supporting evidence in the fact that there is a regressive element in humour that has been pointed out by Freud (1960) and others (eg: Keith-Spiegel, 1972). Also of note is McComas' (1923) proposal that laughter became strongly developed in human beings because during the

long period of parental dependency infants required signals to control and reward care-taking by the parents and elder peers.

As has been mentioned, one of the key factors in this proposed neotenous aspect was the prolonged period of parental care that existed in hominin society relative to their ancestors. Analysis of dental fossils (which is acknowledged to be superior to other forms of skeletal analysis in terms of determining growth and development (Smith et al., 2007)) suggests that extended childhood had reached levels similar to those of modern humans by the time of Homo Antecessor (0.8 – 1.2 MYA) (de Castro et al., 2010). Childhood is more specifically defined by Bogin as "the period following infancy, when the youngster is weaned from nursing but still depends on older people for feeding and protection" (1997, p.62). In evolutionary terms this scenario would have provided an environment of relaxed selection, which is reminiscent of the "appropriate emotional climate" that Paulos refers to (2008) and is also one of the prerequisites for the emergence of humour cited by Arthur Koestler: "a relative security of existence, which called for new outlets of excess energies" (1964, p.63). Within the proposed model, prolonged childhood provided an extended period of relaxed selection[31], which allowed play to occur with older, more cognitively developed children. This, in tandem with the related increase in neural plasticity (as per Goyal et al., 2014), would have facilitated the emergence of a more cognitively advanced form of smiling/laughter stimulus (i.e. humour) and provided an ideal environment for such behaviour and related information to be shared between peers.

Aside from the specific aspect of the related increase in brain plasticity, relaxed selection is seen to be conducive to the emergence of novel behaviours because "(t)he number of evolutionary pathways available to a species is constrained when movement to an adjacent evolutionary point involves a loss of Darwinian fitness" (Foley & Lee, 1989 p.903). As such, a scenario involving relaxed selection has the potential to allow a broader palette of behaviours to potentially emerge. Roger Lass has summed this up by saying: "(b)y not insisting on the 'utility' of all parts of an organism, but allowing for 'nonaptations', features with no synchronic function, not doing anything, they permit organisms the freedom to evolve" (1990 p.81). This helps to explain how laughter, a noisy and slightly debilitating convulsion that had the potential to attract

[31] The term "relaxed selection" refers to a reduced level of selective pressures, for a general overview see Lahti et al., 2009

predators, managed to find its initial evolutionary niche. The common idea of being weak or helpless with laughter is supported by research showing that there is decreased muscle tone during laughter (Paskind, 1932) and this adaptively negative side effect adds to the mystery of why such a feature would have evolved and considering relaxed selection helps to reconcile this.

Deacon's paper "(a) role for relaxed selection in the evolution of the language capacity" (2010) is particularly relevant to this topic. In it he refers to a process of evolutionary potential and exaptation proposing that there are periods of selective relaxation and pressure causing an expansion of potentials followed by the realization of those potentials. He notes that some traits emerge serving a specific role in a specific circumstance, and later on perform completely different functions (i.e. they are exaptive). In a situation of relaxed selection there is greater potential for the emergence of a wider variety of traits to emerge, and future circumstances and constraints serve to determine what adaptive values these traits may or may not have. If a behaviour lacks an immediate synchronic adaptive value but instead, becomes adaptively beneficial at a later point in evolution this can be referred to as exaptation, and the resulting products are sometimes referred to as spandrels. An exaptation is defined as: "a feature, now useful to an organism, that did not arise as an adaptation for its present role, but was subsequently co-opted for its present function" (Gould, 1991, p.43). The term was introduced by Gould and Vrba (1982) to help to explain evolutionary changes with little to no immediate adaptive value, and to eliminate the teleological implications of the previously used term "pre-adaptation". The idea that adaptive values shift over time due to changes in the individual and their environment is particularly relevant to complex behaviours such as humour and language because of the progressive stages involved in their evolution and the evolution of relevant ecological factors. Language is a good example of this because the adaptive value of its fully evolved form is self-evident, but determining the adaptive value of the steps that would have been required in order to achieve that evolved state has been a troublesome process (for a summary see Bickerton, 2009).

Returning to the topic at hand, it can be seen that a condition of relaxed selection would have had the potential to promote novel phenotypes such as humorous behaviour inclusive of any related genetic aspects and/or modes of genetic expression, which translated into increased phenotypic plasticity (as per Agrawal, 2001). This assertion is supported by the research of Hunt et al. who stated

> genes evolving under relaxed purifying selection may more readily adopt new forms of biased expression during the evolution of alternate phenotypes. These results suggest that relaxed selective constraint on protein-coding genes is an important and underappreciated element in the evolutionary origin of phenotypic plasticity (2011, p.15936).

Returning to neurology, the synaptic structures of hominin infants and children involved in humorous play would have been in a developmental stage involving gene expression related to synapse formation and neurite growth. During the course of this phase of childhood development, it has been observed that synapses that operate together typically end up having strengthened connections (Hensch, 2005; Miller, 1996; Schatz, 1990). This process is sometimes summed up by the phrase "what fires together wires together" (eg: Schatz, 1990)[32] and it is a factor in natural selection because the phenotypic aspects that are promoted during this developmental phase will necessarily have some relationship with the individual's ability to survive and/or reproduce: "moderate amounts of (adaptive) plasticity are optimal for evolution in novel environments" (Price et al., 2003).

In terms of the cognitive/behavioural aspects related to the proposed scenario, the dynamics of relaxed selection would have allowed for an individual to operate in an autotelic state (i.e. without extrinsic telos[33]) and Apter and Smith have discussed this in relation to both play and humour (1977). Simply put, telic behaviour is goal-oriented and involves lower levels of arousal while paratelic/autotelic[34] behaviour is based on its own perceived merits regardless of any specific goal(s) and occurs during higher states of arousal: "When the individual is in a paratelic state, he behaves because he enjoys the behaviour in itself and, where goals are involved, these are…inessential" (Apter & Smith, 1977, p.96). Relaxed selection would have facilitated situations favouring autotelic behaviour, and within the proposed model humour represented an autotelic cognitive operation that was social and communicative in nature. Other similar

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[32] "What fires together, wires together" can be seen as the application of Hebbian learning in neural networks (Munakata & Pfaffly, 2004)
[33] Telos is defined here as a goal or purpose.
[34] "Paratelic" indicates an absence of telos, whereas "autotelic" refers to intrinsically generated telos. In both cases there is an absence of extrinsic telos which allows for the cross-comparison that is made, though it is emphasized that the terms are not being conflated.

examples of such autotelic cognitive operations include music, visual art and other manifestations of the aesthetic impulse, which are worthy of further consideration. It is however, possible to propose that humour was only necessarily autotelic when it occurred spontaneously or reflexively. Voluntary creation of humour involves the goal of eliciting smiling/laughter as well as the possibility of strategic elements that were discussed in relation to conative humour theories, and as a result a telic aspect can potentially be seen. This situation presents something of a conundrum in that the goal of humour would have been to promote the continuation of a non-goal oriented state: its goal was to avoid goals. As such, it could be argued that the goal of eliciting laughter (as opposed to strategic goals) should not be considered to be functionally telic in nature.

6.4.1 Summary

It is proposed that the prolonged childhood of early hominins created a situation of relaxed selection that allowed humour to emerge during the state of moderate arousal, positive emotion and autotelia experienced during play. As such, humour at its point of emergence was a non-goal oriented spontaneous and/or reflexive perceptual behavior that existed primarily during childhood and eventually evolved to become potentially goal oriented and present in all age ranges (i.e. it was neophilic). Early hominin humour would have been experienced primarily or entirely during childhood, when patterns of behavior and their related neurological activity and gene expression were at their greatest level of plasticity, and any beneficial resulting phenotypic changes in these regards[35] had the potential to play a positive role in the ability of individuals and groups to survive and/or reproduce. Early humour differentiated itself from other forms of smiling/laughter stimuli because it was derived from the cognitive processing of specific events and once it evolved to a point where it was produced voluntarily it provided a framework wherein individuals could communicate and share with others the experience of a specific cognitive event and the associated emotional state.

Having now considered the neotenous nature of humour as well as important related aspects such as its autotelic dynamic, it is now possible to move on to mapping out a logical step-by-

[35] A discussion of the rewards and benefits of humour is on pp. 67-76

step causal sequence of behaviour related to the evolutionary emergence of humour. The following section is of critical importance in providing a clear picture of the topic that considers the evolution of behavioural development rather than abstracted theoretical concepts.

7 Evolutionary stages in early humour

7.1 Approaching a step by step model of the evolution of early humour

In the preceding chapter it was asserted that humour emerged during play as a more cognitively particulated manifestation of previously existing laughter/smiling stimuli. Within the proposed model the first examples of humour would have been accidental/incidental and thus, were based on perception and cognition without any element of voluntary creation. It is logical to propose that over the course of time there would have been reflexive repetition of specific acts of accidental humour, followed by habituation and ultimately, the rational, intentional recall and performance of specific humorous acts. Rather than rely on such a general statement, however, it is more scientifically rigorous to try and determine what simple progressive steps may have occurred in this development of humour, and what the cognitive and social ramifications of this progression might have been. By considering basic cognitive, psychological, social and ecological dynamics involved, it has been possible to inductively determine the possible evolutionary progression of humour that follows. I will first present a brief summary of the proposed steps, and then examine each step in sequence and in so doing, review the factors that were considered in the inductive process.

1) Accidental/Incidental. An individual spontaneously displayed a specific action or sequence of actions during play that caused smiling/laughter spectrum response(s) in one or more others.

2) Repetition in situ. An individual spontaneously displayed a specific action or sequence of actions during play that caused smiling/laughter spectrum response(s) in one or more others and subsequently, reflexively driven by physiological, psychological and social rewards, immediately repeated the action, possibly several times. This would have begun as a reflexive process but eventually would have become habituated and voluntary.

3) Imitation by a second party in situ. An individual imitated a spontaneous or repeated action

of another individual that stimulated smiling/laughter spectrum response(s). This would have begun as a reflexive expression but eventually would have become habituated and voluntary.

4) Repetition from memory. Driven by rewards, an individual repeated their own spontaneous or repeated (more likely repeated) action that had stimulated smiling/laughter spectrum response(s) on a previous occasion. At first, the gaps between repetitions would have been small; a humorous action might be repeated within the same session of play but with a notable gap of time between the two performances. Eventually recall would have occurred in separate episodes of play within the same day, then on separate days etc. Rewards were yielded for the improvement in memory recall. This stage, and all subsequent stages involved voluntary expression.

5) Repetition from memory by a 2nd party. Driven by rewards, an individual imitated another individual's spontaneous or repeated (more likely repeated) action that had stimulated smiling/laughter spectrum response(s) on a previous occasion. The dynamics of increased time gaps involved would have been similar to those outlined in stage 4.

6) Accidental variation. Repetition (especially those from memory) and imitation produced actions that were not true copies of the original. Some of these variations were humorously successful and thus, continued to be replicated in their evolved form; imitated by others who had the requisite capacity of memory and expression.

7) Combination and reconfiguration. Rewards stimulated the intentional creation of variations involving different combinations as well as the isolation of specific elements.

8) Ideation. Novel actions were ideated and performed with the intention of stimulating smiling/laughter spectrum responses. Initially these would have been in some way associated with previously experienced humorous actions and/or their specific elements but they would have become increasingly independent.

Ideation does not by any means represent the end of the evolution of the dynamics of humour but it completes the transition that humour makes from being limited to the perceptive/cognitive appreciation response to the point where it was intentionally created and performed, in part as a result of the role of rewards and benefits.

7.2 Rewards and Benefits

The preceding list of stages places emphasis on the role of rewards and as such, before looking at the stages in more detail, it is first necessary to address the subject of rewards and the related, but distinct, subject of benefits. Roll's definition of rewards ("anything for which an animal [which includes humans] will work") (2011, p.1) will be employed in this thesis, and benefits will be given the general definition of anything that contributes to an individual's ability to survive and/or reproduce (i.e. anything of adaptive value). There is, of course, overlap between these two categories: behaviours that provide rewards have the potential to yield adaptive benefit, but it is also possible for rewards to be adaptively neutral or deleterious. It should also be remembered that the conscious recognition of a benefit will cause it to also function as a reward: if an individual is able to determine that a specific behaviour yields a specific benefit (or benefits), then that benefit may become something for which they will work.

Rewards

In keeping with the fundamentals of Darwinian theory, evolutionary studies have typically been primarily focused on the notion of adaptive values[36] rather than rewards (e.g. Dissanayake, 2009; Fredrickson, 1998; Levins, 1962) and Tooby and Cosmides have described adaptive theories as "an indispensable methodological tool, crucial to the future development of cognitive psychology" (1994, p.844). There have also been arguments that adaptive function should not be the sole focus of research, such as in Gould's criticism of evolutionary psychology where he refers to "the blinkered view that evolutionary explanations must identify adaptation produced by natural selection" (from Kalant et al. 1997 p.2). Bearing in mind such criticisms and the autotelic nature of humorous behaviour it is reasonable to put substantial emphasis on the aspect of rewards. I have already established that Roll's definition of reward will be applied ("anything for which an animal (which includes humans) will work") and it is helpful to consider his explanation of the operation of reward-driven behaviour:

[36] "Adaptive value" is defined as the usefulness of a heritable trait that can help an organism to survive/reproduce in its environment.

> (s)ome stimuli are unlearned reinforcers (e.g. the taste of food if the animal is hungry, or pain); while others may become reinforcing by learning, because of their association with such primary reinforcers, thereby becoming 'secondary reinforcers'. This type of learning may thus be called 'stimulus-reinforcement association', and occurs via a process like classical conditioning. If a reinforcer increases the probability of emission of a response on which it is contingent, it is said to be a 'positive reinforcer' or 'reward' (1990, p.162).

Put simply, rewards create a motivation/drive that causes an individual to repeatedly engage in a specific behaviour. The existence of this drive helps to explain why during the course of evolution, a behaviour might have proliferated despite having limited adaptive value, being adaptively neutral, or even having deleterious adaptive effects[37]. In the case at hand, substantial rewards would have contributed to the continuation/proliferation of humour even if there were no associated adaptive benefits[38].

Humorous behaviour facilitates rewards because it is an emotionally mediated process:

> The emotional route to action is flexible not only because any action can be performed to obtain the reward or avoid the punishment, but also because the person can learn in as little as one trial that a reward or punishment is associated with a particular stimulus, in what is termed 'stimulus-reinforcer association learning'. (Rolls, 2013 p.7)

As such, behaviour driven by emotional rewards is associated with an accelerated learning process, which is worthy of further consideration, but before getting to that point it is necessary to be more specific regarding what rewards may reasonably be attributed as having been yielded by humorous behaviour. Mobbs et al., 2003 state that reward is "the most fundamental feature of humor" (p.1041) and folk wisdom since the late nineteenth century has increasingly asserted that humour is positive and desirable (Apte, 1985). This view is supported by qualitative and quantitative research that has documented the various rewards triggered by humour and its associated smiling/laughter responses. The list of rewards that follows is

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[37] The proposed dynamic is made possible in part by the situation of relaxed selection that has already been attributed as a situational component of early humour.

[38] Humour did have adaptive benefits and they will be discussed shortly, but this description is given to illustrate the importance of rewards.

intentionally précised and there is no critique offered in relation to the research underlying it[39]. The list also deliberately cites rewards that apply to varying categories such as physiology, individual behaviour and social behaviour. While this may appear somewhat incohesive, the purpose of the list is simply to demonstrate in broad terms that humorous behaviour has, (and would have had) the potential to act as a trigger for various endogenous and exogenous rewards. These rewards include but are not limited to:

i) an elevated mood caused in part by stimulation of the nucleus accumbens (NAcc), ventral tegmental area (VTA), and amygdala, triggering the mesolimbic dopaminergic reward system (Mobbs et. al, 2003) and the release of β-endorphins (Miller & Fry, 2009). Related to this there is an elevation in the pain threshold (Dunbar et al., 2011; Weaver & Zillmann, 1994; Weisenberg, Tepper, & Schwartzwald, 1995) caused by endogenous opioid release in the thalamus, caudate nucleus, and anterior insula (Manninen, 2017). This type of opioid release also serves to stimulate enhancement of the reward effect for food and drugs (Henriksen & Willoch, 2007, Nummenmaa & Tuominen, 2017). Mobbs et al., 2003 also note activation of the temporo-occipital junction, IFG/temporal pole, and SMA/dACC in the left hemisphere and this pattern of left-lateralization has been observed in monetary and video-game reward tasks;
ii) regulation of dopamine and serotonin levels causing a positive effect on emotional states and patterns of emotional states (Ashby & Isen, 1999; Cha & Hong, 2015);
iii) preparation of the body for action (which is relevant to play situations) through an increase in heart rate and adrenaline levels (Levi, 1965);
iv) a reduction in anxiety (Cann et al., houn 1999; Yovetich et al., 1990), tension (Wooten, 1996), depression (Falkenberg et al, 2011; Deaner & McConatha, 1993) stress levels due to decreased levels of cortisol and epinephrine (Berk et. al, 1989; Nezu et al., 1988);
v) an increase in self-esteem (Frecknall, 1994; Kuiper et al., 1992), and a sense of empowerment and control (Sherman, 1998; Wooten, 1996);
vi) an increased ability to initiate, maintain and enhance interpersonal relationships (Smoski & Bachorowski, 2003; Salovey et. al 2000; Lefcourt, 2001);
vii) a reduction in levels of hostility in social groups (Collinson, 1988).

[39] Further consideration of the listed rewards in an evolutionary context will be given at different points in the text later in the thesis.

It could be argued that many, if not all, of the preceding rewards can be seen as providing some measure of adaptive benefit, but even if no adaptive benefit was yielded, the element of reward would still have stimulated repetition of the behaviour. The listed rewards also have some degree of overlap, for example, the release of endogenous opioids involves the mesolimbic dopaminergic reward system and may be a contributing factor in social rewards (Nummenmaa et al., 2015; Panksepp et al., 1981). While the recent research of Manninen et al. (2017) has helped to provide valuable information regarding the opioid aspect of the neurochemical results of laughter/humour, a comprehensive picture of the neurochemical dynamic and its associated behavioural aspects is not yet available.

While considering neurochemical aspects, it is notable that there has been credible speculation that laughter stimulates oxytocin production (Devereaux et al. 2007). Even though, to my knowledge, there has been no direct research on this[40], it has been proposed that the release of oxytocin and endorphins may be triggered by similar stimuli (Carter, 1998; Uvnas-Moberg, 1998, Dunbar, 2004) and the notion that laughter stimulates oxytocin production is also supported by fMRI studies showing that smiling/laughter spectrum responses cause an increase in activity in the hypothalamus, which is the primary area of oxytocin production (Schwartz et al., 2007). The hypothesis that producing and/or hearing laughter stimulates oxytocin production remains speculative at this time but indicators are positive enough to consider the ramifications of this. If such research confirms the hypothesis, it will link humour/laughter with neurochemically stimulated social bonding, physical development of the neocortex, and social learning (Carter, 2014). In an evolutionary context, the stimulation of oxytocin production through humorous behaviour would have provided both reward and benefits. Research into humour/laughter and other neurochemical activity (eg: relating to vasopressin, pheromones, GABA) may also be of potential interest.

The noted crossover between different rewards does nothing to reduce the essential information that can be gleaned from clinical research: humour and its associated smiling and laughter responses have the potential to produce a powerful combination of rewards that would have

[40] The lack of research in this direction was confirmed in personal correspondence with Paul Zak (Claremont University).

served to stimulate the repetition of humorous behaviour in hominin populations. There is also an underlying physiological component that would have contributed to a dynamic of perpetuation of specific behaviours that can be seen by correlating the findings of two separate research projects. Schachter and Wheeler's (1962) research showed that increasing the level of arousal of the sympathetic nervous system by way of an injection of epinephrine increases levels of humour response, while Levi's (1965) research showed that the experience of humour increases adrenaline levels which increase the level of arousal of the sympathetic nervous system. So it can be seen that humour stimulates arousal, which then facilitates further humour, which stimulates arousal, etc. It is acknowledged that this dynamic is not infinite, and aspects relating to cognition (e.g. attention), physiology (e.g. fatigue), psychology (e.g. disruption in positive emotional valence), social dynamics (e.g. negative influence by other individuals), situation (e.g. the appearance of danger) etc. would ensure that humorous episodes were finite. Despite such modulating factors, there would still have been an autocatalytic mechanism at work: once humour was initiated, its functional dynamics would have stimulated an increased receptivity to subsequent humour. This dynamic represents a physiologically rooted positive feedback loop and can be related to the positive upward spiral described by Fredrickson & Joiner (2002)[41], which provides further evidence of the potential for a positive relationship between humour and social learning. Put simply, positive emotional states facilitated humour, which stimulated positive states, which facilitated humour etc.

It is important to recognize and differentiate all the potential rewards that may have been associated with humorous behaviour, but the role of dopamine and the meso-limbic reward system is primary among them due to its direct and immediate nature[42]. As such, it would have been necessary for the hominins in question to have had the capacity to produce the requisite levels of dopamine, and an increase in the capacity for dopamine production did occur in hominins as early as 1.9 MYA in part due to dietary factors (DeLouize et al., 2017). Emphasis on dopamine and the meso-limbic reward system is also justified because these rewards would have been more direct than the more dynamically complex social rewards that are listed, which have the potential to be quite complex, though play-related joy has been observed to play a role

[41] The theory proposes that positive emotions broaden the scopes of attention and cognition, thereby facilitating the building of personal resources and initiating upward spirals toward increasing emotional well-being.
[42] If a link between laughter and oxytocin production is established it will be a direct and immediate reward effect that is significant and distinct from dopamine and the meso-limbic reward system.

in social facilitation and bonding in many less cognitively developed mammals (Panksepp & Burgdorf, 2003). It could also be argued that in keeping with its element of ambivalence, humour does not always have a positive effect on social relationships and this has been shown in studies of negative and aggressive humour (Martin et al, 2003; Yip & Martin, 2006). This type of humour, however, is more likely to have been the exception rather than the rule as is demonstrated in ontogenic evidence showing that children typically display more affiliative than non-affiliative humour (Groch, 1974). Further support for the idea that humour would have tended to be primarily affIliative is the underlying prerequisite of a positive emotional valence, which is affirmed in temperament based studies that characterize humour as involving a combination of high trait cheerfulness, low seriousness (high playfulness), and low bad mood, as measured by the trait form of the State-Trait Cheerfulness Inventory (STCI) (Ruch & Kohler, 1998; Ruch et al., 1996).

It is also worth noting that negative and aggressive humour can also be seen to have functioned as a way of allowing aggression to be displayed without resorting to physical violence and this could potentially have yielded rewards and been of some adaptive value. Berk outlines this type of dynamic when he states

> Using humour involves a cognitive shift in perspective that allows one to distance oneself from the immediate threat of a problem situation; that is, view it from a different frame of reference and reduce the negative feelings that would normally occur (2001 p.326).

In summary, there is substantial empirical research evidence demonstrating that numerous rewards are stimulated by humour and its associated smiling/laughter spectrum responses. It is proposed that these rewards caused humour to operate in an autocatalytic fashion that resulted in the continuation and proliferation of humorous behaviour after its initial point of emergence within groups. As such, the emergence of humour was representative of the transition in hominin evolutionary dynamics from the purely biological to the bio-cultural: from the properties of people to the relations between people. Other animals ability to survive and reproduce was dictated by biology and environment, but hominins were able to exert influence in this regard through social/behavioural means. In simple terms, at the earliest stages of humour's emergence, the rewards yielded by humour can be seen as the engine that drove its repetition and continuance. Rewards are the key element in the proposed autocatalytic dynamic and their

importance represents a significant departure from the typical benefit based notions that can be seen in other considerations of humour in an evolutionary context.

Benefits

In the preceding section it was shown how rewards would have ensured the continuance and proliferation of humorous behaviour in hominins regardless of adaptive benefits involved. The purpose of showing this was not to underplay the role of adaptive benefits, but simply to emphasize: i) that humour was not entirely evolutionarily dependent upon them, and ii) that the dynamics of the reward system within a social framework represented an evolution in the process of evolution itself.

Adaptive benefits differ from rewards in that they do not necessarily serve to directly motivate behaviour, though once an individual associates a benefit with a behaviour it has the potential to become a reward. In the case of mate selection, for example, the correlation with humour may not be immediately evident: a single instance of humour tends not to trigger an immediate request to engage in sexual intercourse (if it did, comedy clubs would be very different places). Over evolutionary time however, the observation that humour was pro-social and enhanced prospects of mate selection, would have gradually been made and after this point mate selection would have necessarily functioned as a reward as well as an adaptive benefit. Reeve and Sherman define an adaptation as "a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment" (1993 p.9). There have been a number of potential adaptive values of humour proposed by theorists, some of which were reviewed in chapter three, but a more comprehensive list will now be presented[43]. I have tried to ensure that the list of benefits that follows includes only benefits that would have been applicable in an evolutionary context; but some that are included, such as the one relating to energy expenditure and obesity (Buchowski, 2005), probably relate more directly to a contemporary context. For the sake of organizational efficiency the list also includes benefits specifically applicable to humour after the evolutionary point where it passed through its proposed initial neotenous phase and became part of adult behaviour. Primary among these is

[43] All the rewards from the list in the preceding section can, to a greater or lesser extent, be considered to have some potential adaptive benefit and, as such, could be added to the following list of benefits.

the role of sexual selection, which will be considered in more detail in a later chapter[44]. There will be no in-depth analysis of the contents of the following list, it is merely intended to be a tool to demonstrate the depth and breadth of acknowledged benefits of humour/smiling/laughter that could have played some role, large or small, in the survival and/or reproduction of hominins during the course of their evolution. This approach serves to address the fault of limiting evolutionary significance to a single benefit and adds to the academic literature a reasonably comprehensive list of adaptive benefits. As with the preceding list of rewards the list of benefits that follows is intentionally précised, there is no critique offered in relation to the research underlying it[45] and it cites rewards in varying categories such as physiology, individual behaviour and social behaviour. The clinically documented benefits of humour and its associated smiling/laughter responses include but are not limited to:

i) improved mental functioning (Derks, Bogart & Gillican, 1991; Sveback, 1982), which is caused in part by increased catecholamine levels (Fry, 1984);
ii) improved memory in both recall and recognition (Carlson, 2011; Krishnan, 2003; Schmidt, 1994; Summerfelt, Lippman & Hyman Jr., 2010);
iii) activation of neural imitation systems (Leslie, Johnson-Frey & Grafton, 2004) and "mirror neurons" (Krolak-Salmon et al., 2006; Warren et al., 2006) (for a review of the possible role of mirror neurons in hominin evolution see Ramachandran, 2000);
iv) improved immune functioning due to an increase in T cells (Berk et. al, 2001), increased levels of Immunoglobulin A (IgA)(Dillon, Minchoff & Baker, 1986, Lefcourt, Davidson-Katz & Kueneman, 1990), an increase in the flow of the lymphatic system (Shields, 1992) and the production and activity of NK cells (Bennett et al. 2003, Berk et. al 2001);
viii) improved respiratory functioning, reduced possibility of pulmonary bacterial growth, (Fry, 1994) and reduced effects of bronchial asthma (Kimata, 2004(a)) and obstructive lung disease (Brutsche, Grossman & Muller, 2008);
ix) modulated levels of serum pro- and anti-inflammatory cytokines in patients with rheumatoid arthritis (RA), varying depending on the RA disease activity (Matsuzaki, 2005);

[44] See pp. 164-168.
[45] Further consideration of the listed benefits in an evolutionary context will be given at different points in the text later in the thesis.

x) reduction in allergic responses associated with atopic dermatitis due to reduced plasma levels of nerve growth factor (NGF), brain-derived neurotrophic factor (BDNF), neurotrophin-3 (NT-3), neutrophin-4 (NT-4), allergen-specific IgE and cytokine (Kimata, 2004(b), Kimata, 2004(c); Kimata, 2004(d));

xi) increased levels of breast-milk melatonin in nursing mothers. Feeding infants with milk with increased levels of melatonin reduces allergic responses in infants (Kimata, 2007), enhances adaptation to circadian rhythms (Illnerova et al., 1993), improves infants' sleep and reduces infantile colic (Engler et al., 2012);

xii) amelioration of post-prandial glucose excursion in diabetics (Hayashi et al., 2003) and mitigation of diabetic nephropathy due to modulation of prorenin receptor gene expression (Hayashi et al., 2007);

xiii) increased energy expenditure (10–15 min of laughter increases energy expenditure by approximately 50–170 kJ (10–40 kcal))(Buchowski, 2005), which could be of particular benefit to obese individuals or those with reduced mobility;

xiv) lowered risk of myocardial infarction (Clark, Seidler & Miller, 2001) and reduced risk of recurrence (Tan et al., 2007), in part due to reduced arterial wall stiffness (Vlachopoulos et al., 2009) and improved endothelial function (Sumawara, Tarumi & Tanaka, 2010);

xv) an increase in empathy (Hampes, 2001), intimacy (Hampes, 1994), and interpersonal trust (Hampes, 1999);

xvi) enhanced infant/parent bonding (Riem et al., 2012; Provine, 2001) helping to ensure survival into adulthood;

xvii) an increase in sexual desirability (Bressler, Martin & Balshine, 2006; Greengross & Miller, 2011; Kaufman et al., 2008; Li et al., 2009);

xviii) positive modulation of depression (Ashby & Isen, 1999; Cha & Hong, 2015; Ko & Youn, 2011; Morgan & Jorm, 2008);

xix) an increased rate of pregnancy (Friedler et al., 2011)/enhanced fertility level (Chung, 2011);

xx) increased longevity (in association with smile intensity) (Abel & Kruger, 2010).

In addition to these clinically documented benefits there are also other theoretical benefits that have been proposed by various academics. A comprehensive examination of these is beyond the scope of this thesis but the authors have cited clinical evidence in varying degrees to support their theories. These theories have tended to focus on benefits that are the result of complex combinations of social, psychological and behavioral aspects. These benefits include:

a. a coping mechanism to build resilience and alleviate the negative effects of struggles, tragedies and disappointments (Berg & Van Brockern, 1995; Carlson & Peterson, 1995; Kuiper, 2012);
b. an improved quality of life (Lebowitz et al., 2011);
c. improved information processing ability (and associated benefits)(Hurley, Dennett & Adams, 2011);
d. a higher level of general intelligence (Greengross & Miller, 2011; Hauck and Thomas, 1972; Howrigan & McDonald, 2008; Miller, 2000(a)).

Also, the role of Theory of Mind (see pp.85-86) in the functional dynamics of humour evokes a more general beneficial dynamic summed up by Knight et al. "natural selection favours increasingly complex systems of perceiving and representing the world. This is because enhanced sensitivity to aspects of the environment predictably affords an animal advantages over its fellows" (2000 p.4). In sum, there is a substantial list of potential adaptive benefits for humour in an evolutionary context.

It should be noted that humour and its related smiling/laughter responses do also have a small number of reported negative effects. These are limited both in number and in frequency and they include incontinence (Herms et al., 2006), syncope (fainting) (Amaki et al., 2007; Bragg, 2006), and in some rare cases laughter can cause headaches (Levin & Ward, 2003) or a dislocated jaw (Chan et al., 2008). There can also be adverse cardiovascular effects such as conduction anomalies (Chow et al., 2012) and even cardiac rupture (Locke, 1927) caused by more intense bouts of laughter. These negative effects, however, tend to be of minor significance and/or are the result of extreme laughter episodes and/or pre-existing medical conditions. It is reasonable to concur with Ferner & Aronson's assertion in the British Medical Journal that "laughter in any form carries a low risk of harm" (2013 p.f7274).

Conclusions

The preceding lists of rewards and benefits provide substantial research-based support to the common sense notion of the positive nature of humour. The volume of benefits with potential adaptive value supports the notion of a holistic approach rather than simply identifying a single

benefit as being the one that explains the role of humour in relation to natural selection. To that end it is proposed that for hominins engaged in humorous behaviour:

i) rewards were yielded that provided a behavioural drive that aided in the continuance and proliferation of humorous behaviour and ensured that humorous behaviour and any associated broader mechanisms it may have stimulated were able to function and evolve in an autocatalytic manner and
ii) adaptive benefits were stimulated that ensured that individuals and groups involved in humorous behaviour were preferred in the process of natural selection (related to both survival and reproduction).

It is proposed that the continuation and proliferation of humorous behaviour following its point of emergence was contingent on a combination of rewards and benefits, and that in evolutionary terms it was the rewards and benefits stimulated in hominins that determined whether a specific behavioral phenotype was able to replicate itself and flourish in the face of the pressures of natural selection. While it can be seen humour would have had numerous adaptive values, it also is both novel and important to recognize the significance of rewards in relation to evolutionary dynamics, as well as in terms of gaining a more comprehensive understanding of the complex dynamics of humour. Rewards were the engine that drove continued patterns of humorous behaviour, and benefits ensured that individuals demonstrating such behaviour were more likely to survive and reproduce; it was a powerful evolutionary combination.

7.3 Stages in the emergence of humour

Bearing in mind the roles played by rewards and benefits, I will now examine in more detail the previously outlined stages in the emergence of humorous behaviour. I am aware that these stages are necessarily speculative but they represent a logical hierarchical evolutionary progression based on a causal sequence, and supporting evidence is given whenever possible. This section of the thesis is of particular importance in that it proposes a specific causal sequence of behaviour and cognition, which makes it unique within the existing literature and demonstrates potentially practical aspects that complement the more abstract theoretical ones. I will begin by looking at the specific behaviours involved in each stage and discuss the cognitive ramifications of these behaviours, and then examine in some detail the more general social and behavioural ramifications of the widespread general use of humour in hominins. One consistent

thread in the following progression is the dynamics between rewards/benefits and cognitive, communicative, and social aspects of hominin life. For example, I will be discussing the role of memory in the creation and appreciation of humour, and illustrate how improved retention and recall of memories would have stimulated rewards and benefits. In broader terms the mechanism of humour served to provide rewards and benefits not only for humorous behaviour but also, by default, for any/all associated cognitive, behavioural, communicative and social aspects.

It was stated earlier that the point at which humour emerged was when laughter was stimulated by the perception/cognition of specific actions: when a specific action became the stimulus rather than a general state/situation. It is logical that the first examples of this would have been the most cognitively simplistic ones possible and as such, we can remove intentionality from the equation and assume that humour began as a perceptual/cognitive event. Accordingly, Stage 1 is termed “Accidental/Incidental”.

Stage 1 – Accidental/Incidental

> Summary: an individual spontaneously displayed a specific expression or sequence of expressions during play that stimulated a smiling/laughter response(s) in one or more others.

As was mentioned before, this scenario stands in contrast with Provine’s (2001) hypothesis that the first instance of humour may have been a feigned tickle, which it was asserted is a more cognitively advanced process. Another possible origin of humour that can be ruled out is stimulation by antiphonal laughter, which would have been an evolutionary dead-end because non-Duchenne laughter is not contagious in the way Duchenne laughter is (Provine, 1992) so unless the non-Duchenne laughter was in some way contextually incongruous this scenario was not a viable one. As such, no form of intentional stimulus could emerge because once it became intentional, it would cease to function as a stimulus. Instead we must look to other possible actions (including vocalizations) as being the initial source of humour. The factors that would have facilitated the potential of a stimulus were positive emotional valence, moderate arousal, and association with laughter/smiling and perceived incongruity. Essentially, humour was most likely to have been experienced in a situation where an individual was happy and excited, laughter was at least occasionally occurring, and an easily perceived incongruity took place.

Bearing these factors in mind, an episode involving a specific unexpected action representing the threat of tickling is a likely candidate, but any number of surprising (i.e. incongruous) actions that took place within the positive emotional climate of play are also possible. In terms of a possible ontogenic parallel, human infants laugh at a wide variety of unexpected stimuli that occur in non-serious contexts (McGhee 1976; Sroufe & Waters 1976). It is possible that the first instances of humour occurred during chasing games, due to the elevated state of arousal, but the lack of face-to-face contact suggests this was likely not the case. Babies also display a predisposition (possibly sub-cortical) to looking at faces (Mondloch et al., 1999; Morton & Johnson, 1991), so it is possible that a surprising (in terms of configurations/and or context) facial expression was the culprit. One example of this is peek-a-boo, and the fact that it is a universally observed behaviour (Kleeman, 1967; Maurer, 1969) that can be taught to apes in captivity (Patterson & Gordon, 2002; Savage-Rumbaugh et al., 1985) does suggest the possibility of this type of ancient origin albeit in an accidental framework.

It is neither possible nor necessary to determine what specific action initiated the first instance of humour but within the proposed model it can be seen that the event:

i) took place in a play situation involving two or more children and an elevated level of arousal;
ii) was triggered by a specific action that was accidental/incidentalrather than intentional;
iii) involved the cognition of a perceived incongruity, which triggered a laughter response.

Both laughter and the ability to perceive incongruities existed in hominins before this event occurred, but never before had laughter been stimulated strictly by a perceived incongruity. This first humorous event was made possible by the increased brain size and improved cognitive abilities of hominins relative to their ancestors, and also by the play environment and its associated relaxed selection, which was possible because of the increased period of parental care. This confluence of cognitive and social factors would have allowed humorous behaviour to emerge, and once it had emerged, the dynamics of associated rewards and benefits that has been outlined would have ensured its continuance. Cognitively, this early stage would have involved the perception/cognition of incongruity, and the interpretation of laughter as denoting a positive emotional state, but essentially it was no more cognitively complex than an event where an individual witnessed something frightening and reflexively screamed. Reflecting back on Roll's (2013) work, these two events differ in that the humorous event would have stimulated

rewards that the individual would work to obtain, while the frightening event would have stimulated punishers (i.e. fear) that the individual would have worked to escape from and avoid.

The humorous event in Stage 1 was social in nature and would have been experienced by a minimum of two or more people:

1) the (accidental) creator(s) - the individual(s) producing the action itself who would most likely also witness the humorous reaction to it), and
2) the responder(s) - the individual experiencing the perception/cognition of the incongruity and producing the smiling/laughter response.

All those involved with sufficient capacity for memory could then potentially associate the specific action(s) with smiling/laughter, which could affect the dynamic of both creation and perception of humour in the future. It is also possible that there were proximate individuals who simply witnessed the reaction of laughter, which may have then stimulated antiphonal laughter. These individuals would not have formed an association between the humorous actions and the laughter, but their antiphonal laughter would have contributed to the "affect-induction process that promotes affiliative, cooperative behaviour between social partners" (Smoski & Bachorowski, 2003 p.329). This would not simply have added additional laughter but also amplified the response of the original laughers: "if one person's positive emotional expressions evoke corresponding affect in another the positive expressions thereby elicited in this second party will then amplify positive effect in the original signaller" (Owren & Bacherowski, 2001 p.156). This dynamic shows a type of positive feedback loop, rooted in biology and typically of brief duration, though contagious laughter has been documented to last for prolonged periods (Hempelmann, 2007; Provine, 1992). This is the second feedback loop to be discussed (the first one related to humour and rewards - see p.72) and may be indicative of a pattern of positive feedback loops operating as a result of the dynamics of humorous behaviour.

The presence of antiphonal laughter stimulated by humour was indicative of the fact that humorous events involved emotional sharing, which Rimé describes as having a positive effect: "on emotional climate in general; (2) on group cohesion and solidarity, with positive consequences for emotional climate; and (3) on collective memory, with potential consequences for emotional climate in the long run" (2007 p.307). I have used this quote because of its strong (if somewhat awkward) emphasis on emotional climates. Emotional climate is a much broader notion than the emotional mood of a specific situation: "an emotional climate is more lasting

than a local emotional atmosphere and does not simply refer to collective feeling and behavior but to how the people of a society emotionally relate to one another" (de Rivera, 1992 p.200). Put simply, humour at its point of emergence had the potential to affect the emotional and behavioural dynamics of the group beyond the scope of the actual humorous event itself. It also meant that humorous experiences, by enhancing the emotional climate, increased the likelihood of subsequent humour, not only within the same situation but also within broader social and temporal contexts. This can be seen as an extension of the reward feedback loop described earlier (see p.70).

The presence of antiphonal laughter also meant that humorous behaviour created synchronous social events, and it has been shown that synchronous exertive activities cause a greater increase in pain tolerance than non-synchronous ones, implying a greater release of endogenous opioids, which means that in the context in question the element of synchrony would have amplified some of the rewards that have been outlined. Synchronous behaviour has also been noted to play an important role in social bonding (for a summary see Launay et al., 2016) and, more specifically, it enhances individual's perceptual sensitivity to the actions of others, which increases their success in subsequent joint-action tasks (Valdesolo et al., 2010). It is proposed that this enhancement of competences, as well as the rewards and benefits that were yielded, would have played a positive role in evolving humour past Stage 1.

To recap, Stage 1 involved:

1) children, in a play situation involving positive emotional valence and moderate arousal, perceiving a specific incongruity (or incongruities) in the action(s) of others and/or relating action(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits, which would have fostered the ability to detect breaks in expected patterns of perception and strengthened the association between breaks in expected patterns of perception and a positive emotional state;
2) the potential for the experience of antiphonal laughter, which enhanced the potential of existing rewards and benefits, and added to them improved social memory, enhanced emotional climate, and enhanced perceptual sensitivity to the actions of others, which in turn increased their success in subsequent joint-action tasks.

Stage 2 - Repetition in Situ

> Summary: driven by rewards, an individual reflexively repeated their own spontaneous (accidental) expression(s) that had just caused smiling/laughter spectrum response(s) in one or more others, potentially stimulating further smiling/laughter spectrum responses. Initially this would have been instinctive rather than volitional, but through stimulus-reinforcement association and social learning this would have evolved into a voluntary behaviour over time.

Learning abilities that have been observed in apes (eg: Parker, 1996; Rumbaugh & Gill, 1973) indicate that early hominins were cognitively evolved enough to be aware if their specific action(s) stimulated a laughter response, and once this association was made, rewards would have driven individuals to repeat the specific action(s) in question. In addition to this, it was shown how humorous experiences had the potential to enhance perceptual sensitivity to the actions of others, which in turn would have increased their success in subsequent joint-action tasks (humour itself, being one such task). The feasibility of this type of repetition in the evolutionary context in question is supported in neurological terms by the correlation that exists between the areas involved in humour processing and those involved in re-representation noted by Shammi and Stuss in their work on neural substrates of humour processing:

> Nauta (1973) emphasized the extensive reciprocal anatomical connections of the frontal lobe, particularly with the limbic system, as the basis for its ability to re-represent exteroceptive (information from the outside world) and interoceptive (information from internal milieu/feeling) states. Barbas and Pandya (1989), reviewing the structural and anatomic relationships of the prefrontal cortex, indicated that this region provides the anatomic basis of cognitive–emotional interactions (1999 p.663).

The notion that repetition may have been one of the earliest humorous mechanisms is also supported by its ubiquitous presence in comic performance (Krutnik & Neale, 2006; Sharpe et al., 2014, Zupancic, 2008), which can be seen in infants (Esseily et al., 2016; Reddy, 2001) and throughout the historical records of comedy, both written and oral (eg: Duckworth, 2015; Henke,

1996; Wilner, 1930). Furthermore, Deleuze proposed that humour is actually a core aspect of repetition: "(r)epetition belongs to humour and irony; it is by nature transgression or exception" (1994 p.5)[46]. The entrenchment of humorous behaviour through repetition would have put continued emphasis on the underlying perceptual-cognitive mechanisms and related neurology associated with detecting breaks in patterns of perception and would have strengthened the general association between breaks in expected patterns of perception with a positive emotional state.

The use of repetition would also have enhanced the potential for social learning as repetition has been observed by many scholars to function as a pedagogical tool (for a summary see Matsunobu, 2011). In the context in question, repetition would have aided in the acquisition and proliferation of humour, while also functioning as a comic tool in and of itself. From my own professional comic experience I can assert that repetition can be used as a comic tool by repeating something previously perceived as humorous or by expressing an incongruent repetition: repeating something that is not expected to be repeated. These two methods can also be used in combination. The repetition in question in Stage 2 would have been repetition of something previously perceived as humorous and it was a shared, social experience. Over time, within this scenario, there would have been the gradual creation of a shared body of humorous memories, which, as a result of stimulus-reinforcement association and social learning over time, could eventually be voluntarily expressed.

The ability to produce voluntary (volitional) humorous expressions would have been an remarkable evolutionary achievement, but one that was within the capacity of early hominins as is shown by the limited number of volitional expressions (both gestures and vocalizations) that occur in higher apes (Arbib et al., 2008; Hopkins et al., 2011; Tagliatella et al., 2003). The operation of this reward-driven system stimulating and proliferating behaviour involving voluntary expressions would have been of great importance in making progress towards the emergence of language, in part because it would have involved joint attention. Joint attention is a term that refers to the intentional co-orientation of multiple individuals on a specific locus (Leavens & Racine, 2009) and there has been some debate as to whether it is unique to

[46] It is acknowledged that Deleuze is speaking from a broad philosophical perspective, but the point he makes is still valid and relevant to this passage.

humans or whether it also exists to some degree in apes, monkeys, and domesticated animals such as dogs and horses (e.g. Carpenter & Call, 2013; Tanner & Byrne, 2010; Tomasello et al. 2005) but regardless of this debate it is most strongly exhibited in humans and is associated with the acquisition of language (Baldwin, 1995[47]; Tomasello and Farrar, 1986)[48]. The idea that humour may have served as a mechanism to enhance the capacity for joint attention is also supported by Hutchinson and Turk-Browne's assertion that the stimulation of endogenous (physiological/psychological) and exogenous (social/behavioural) rewards, is important in creating joint attention (2012).

In relation to cognitive evolution it is notable that it has been proposed that joint attention is a precursor to Theory of Mind in ontogenic development (Camaioni, 1992; Tomasello, 1995) and Baron-Cohen's has asserted that there is a valid, if not necessarily strict, ontogenic/phylogenic parallel to be made (Baron-Cohen, 1999). Theory of mind is a term coined by Premack and Woodruff (1978) and it refers to "the ability to attribute the full range of mental states (both goal states and epistemic states) to ourselves and to others, and to use such attributions to make sense of and predict behaviour" (Baron-Cohen, 1999 p.3). Some scholars have claimed that Theory of Mind is central to the operation of humour (eg: Howe, 2002; Jung, 2003) and positive correlations have been shown to exist between humour and the related function of empathy (Hampes, 2001). Ontogenic evidence of a positive correlation between humour and Theory of Mind can be seen in Mireault et al.'s paper (2012) when they cite Reddy's accounts of fake laughter, provocative non-compliance, offer and withdrawal of an item, and provocative disruption of others' activities in infants as young as 8 month old. These behaviours are taken to indicate an understanding of others' minds and intentions (Reddy, 2008) and Mireault et al. conclude that "humour research may reveal that infants are maturing towards developmental milestones like a Theory of Mind at a much earlier age" (2012 p.339).

It should also be added that related to the notion of joint attention is eye contact. Porteus has proposed that smiling and laughter played a significant role in hominin evolution because they

[47] It is valuable to consider Baldwin's notion of intersubjective awareness as a constituent element in joint attention; if two people watched the same tv show at the same time, technically they would meet the criteria of joint attention but they would have no intersubjective awareness.
[48] It is also notable that autism is negatively correlated to both humour (Lyons & Fitzgerald, 2004; Samson et al., 2013), and joint attention (Dawson et al., 2004; Mundy et al., 1990) as well as language acquisition (Eigsti et al., 2011; Mundy et al., 1990).

“represent tension-release systems that have enabled and encouraged sustained face-to-face interaction” (1989 p.281) and adds “the development of highly specific emotional expression in the face played a role in the evolution of speech and of higher-order intelligence” (1989 p.284). In terms of humour, any expression that involved primary emphasis on facial expression or vocalization would have created a situation involving eye contact, and even those that involved primary emphasis on gestures and/or movements and/or objects would still have the potential to produce eye contact due to laughter and smiling. As such, eye contact, which would have already played a role in expressing and assessing communicative intent as is shown by its limited use in higher apes (Gomez, 1996), would have become a behaviour associated with rewards, and thus, would have been stimulated toward further development/evolution. This, in turn, would have increased the potential for hominin communication through facial expression, humorous or otherwise.

So it can be seen through inductive reasoning that in evolutionary terms, there were ramifications of humorous behaviour within broader cognitive and social systems. For example, Charman et al. have stated that “joint attention, play and imitation, and language and Theory of Mind, might form part of a shared social-communicative representational system in infancy that becomes increasingly specialised and differentiated as development progresses” (2000 p.481). As such, humour, by virtue of the fact that it involves joint attention, play and imitation (see pp. 87-88), becomes an integral part of this important developmental system, and this can be seen to be indicative of a possible phylogenic parallel.

At this point it is helpful to present a recap and synthesis of some of the aspects of Stage 2 that have been discussed. Stage 2 involved the act of repetition, which placed continued emphasis on the ability to detect breaks in expected patterns of perception and strengthened the association between breaks in expected patterns of perception and a positive emotional state. The elements of synchrony, repetition, and joint attention that were contributing factors in the dynamics of humorous behaviour (including antiphonal laughter) at this stage (and subsequent stages) should be considered to have constituted part of a shared social-communicative representational system similar to that described in an ontological context by Charman et al. (2000). The operation of this system would have represented an advancement in pro-social behaviour in hominins and resulted in the facillitatation and enhancement of social learning and the promotion of cognitive/behavioural abilities associated with Theory of Mind and the

acquisition of language. Furthermore, this system would have functioned within a positive feedback loop motivated by the rewards and benefits that were stimulated by humour.

To recap, Stage 2 involved:

1) children, in a play situation involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the action(s) of others and/or relating the action(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;
2) the creation, within specific social groups, of shared bodies of memories of humorous experiences;
3) engagement in acts involving repetition and joint attention, which facilitated social learning and advanced the development of Theory of Mind. This process would have yielded mutual rewards and benefits;
4) the continuance and possible strengthening and broadening of the aspects introduced in Stage 1.

Stage 3 – Imitation by a second party in situ

> Summary: an individual imitated the spontaneous or repeated expression(s) of another individual that had previously stimulated smiling/laughter response(s). This would have most likely begun instinctively rather than voluntarily, but through stimulus-reinforcement association and social learning it would have evolved into a voluntary behaviour over time.

In terms of the viability of the preceding, the capacity of apes to engage in imitative and/or pre-imitative (eg: emulation, social facilitation) behaviours (Heyes, 1996; Whiten et al. 1996) is evidence that hominins would have had the capacity to behave in the manner described. It is also notable that it has been asserted that the imitative abilities of apes do not represent true

imitation[49] (eg: Blackmore, 2001; Tomasello & Call, 1997) but are actually simpler pre-imitative forms (which tend to be innate in nature rather than learned). In keeping with this notion, it could be argued that the "imitation" that would have occurred during the emergence of stage three humour should be considered to be a simpler form of "social facilitation" as described by Thorpe: "the performance of a more or less instinctive pattern by one (animal) will tend to act as a releaser for the same behaviour in others" (1963, pp.132-33). Putting aside these semantic considerations, what is important is the idea that humorous behaviour in hominins stimulated the evolution of imitative behaviour in hominins, both qualitatively and quantitatively.

Evidence of the close relationship between humour and imitation is seen in the fact that imitation, much like repetition, is a form of humour in and of itself (eg: Everts, 2003; Alford & Alford, 1981) and it is a form of humour that occurs "more often in simpler societies" (Alford & Alford, 1981 p.158). As such, the following ontogenically based description by Heyes can be considered to be indicative of a reasonable phylogenic parallel in relation to humour in an evolutionary context: "(s)ome human rituals and games may even have the function of promoting the development of imitation; they may have culturally evolved for the 'purpose' of expanding the range of action units that children can imitate" (2016 p.4). The evolutionary significance of this positive correlation between humour and imitation is emphasized by Hurley and Chater's statement that imitation is "a rare ability that is fundamentally linked to characteristically human forms of intelligence, in particular to language, culture, and the ability to understand other minds." (2005 p.1). It is also notable that the presence of imitation also brings with it further connections within social cognitive dynamics between humour and Theory of Mind.

To recap, Stage three involved:

1) children, in a play situation involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the action(s) of others and/or relating action(s) to their body of memories of previous humorous experiences and

[49] Thorpe defines true imitation as "copying a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency" (1963 p.132).

producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;

2) the use of pre-imitative/imitative behaviour and the association of this behaviour with mutual rewards and benefits;
3) the continuance, strengthening and broadening of the aspects introduced in stages 1 and 2.

Stage 4 – Repetition from memory

Summary: driven by rewards, an individual repeated their own spontaneous or repeated action that had stimulated smiling/laughter spectrum response(s) on a previous occasion. At first, the gaps between such repetitions would have been small: a humorous action might have been repeated within the same session of play but with a notable gap of time between the two performances. Eventually recall would have occurred in separate episodes of play within the same day, then on separate days etc. This, and all subsequent stages was/were primarily voluntary.

The viability of the preceding in hominin populations in the evolutionary time-frame under consideration is supported by the documented level of memory capacity in higher apes (eg: Martin-Ordas, 2010; Menzel, 1999) and the ability of 9-month-old human infants to defer imitation over 24 hours (Meltzoff, 1988)[50]. In addition to this, cognitive and behavioural aspects outlined in Stages 1-3 would also have enhanced hominin cognitive and communicative abilities and thus have played contributing roles as well.

Stage 4 can be seen as a progression in a causal sequence which represented a logical extension of the process of repetition: it is repetition plus time. Stages 2 and 3 involved a reward based drive that would have stimulated repetition of humorous expressions, and over time this same drive would have encouraged repetition with time gaps. This process would have both necessitated and rewarded, memory retention and recall. The emotional nature of humorous interactions would also have served to facilitate this process: "(i)mmediately after an emotional

[50] This scenario also implies a capacity for Autonoetic consciousness/awareness: the human ability to mentally place ourselves in the past, in the future, or in counterfactual situations, and to thus be able to examine our own thoughts.

episode, the experience recurs frequently in a person's working memory, increasing his or her thoughts of this experience, and the need to share it" (Rimé, 2009 p.32). Memory retention and recall play an important role in humour and there is a fairly substantial body of research that positively correlates humour with improved memory retention and recall (eg: Chung & Zhou, 2003; Schmidt, 2002; Shammi & Stuss, 1999) as well as research showing similar correlations relating to memory and stand-up comedy performance (Molineux, 2016; Stevens, 2012). With Step 4 the operation of humour involved the yielding of rewards as a result of memory retention and recall, and it is proposed that from Step 4 onwards, humorous behaviour served to accelerate the evolution of hominin capacities in this regard in both quantitative and qualitative terms[51].

It can also be seen that Stage 4 was the point where humorous expressions became unequivocally voluntary in nature. The introduction of volitional humour meant that it became possible for an individual (or group) to control the stimulation of smiling and laughter in others and thus, to control the yielding of associated rewards and benefits. This meant that hominins were engaging in voluntary communication that modified the emotional states of individuals as well as the more general (and long-term) emotional climate of the group, and as such it is proposed that the continued use of humour would have enhanced the ability of individuals to perceive and regulate emotions in others by way of communicative expression. It is also significant that the regulation of emotion involved in humour had a positive valence which would have enhanced co-operation and encouraged pro-sociality. One aspect of this pro-sociality was that voluntary humour typically would have yielded rewards to both the creator and the responder(s): it involved a type of automatic altruism[52].

The importance of Stage 4 can be clearly seen when it is put into context with Social Cognitive Theory as proposed by Bandura[53]. This type of behaviour meant that hominins had become "agentic operators in their life course, not just onlooking hosts of brain mechanisms orchestrated

[51] It is important to clarify/emphasize the fact that when considering the dynamics of humour any/all associated behaviours must be included and thus become potentially constituent to the "humour system".
[52] This automatic altruism in combination with the recognition/communication of taboos meant that humour would have had a significant role in the evolution of hominin morality.
[53] Put simply, Social Cognitive Theory asserts that knowledge acquisition can occur as a diect result of social interactions, by way of an individual observing specific behaviour and its consequences and using information derived from such observation to guide subsequent behaviors.

by environmental events" (Bandura, 1999 p.22), and had minds that were "generative, creative, proactive and self-reflective, not just reactive" (Bandura, 1999 p.23).

The importance of voluntary humour can also be seen in relation to "vocal grooming" (Dunbar, 1998(b), Griebel & Oller, 2008). Vocal Grooming Theory proposes that social vocalizations emerged as a communicative method of strengthening social bonds and in this way, to some degree, it supplanted physical grooming. Physical grooming is slower and requires direct physical contact making vocal grooming a more efficient mechanism (Dunbar, 1993, 2012). According to Dezecache and Dunbar (2012), the increase in efficiency would have been approximately 3:1, and this would have fostered an increase in the size of hominin social groups: individuals would have had the ability to communicate with a larger number of others thus enabling a cohesive social structure in a larger group. Vocal Grooming Theory is partly supported by the body of evidence that suggests that primates use vocalizations as a communicative method of creating social cohesion (e.g. Silk, 2002; Palombit et al. 1999), and Dunbar et al. (2011) believe that laughter was an important form of vocal grooming because it has been shown to stimulate the release of endorphins in humans (see also Nummenmaa et al., 2016) just as physical grooming does in apes, (Keverne et al., 1989) (thus both serve to provide reward). Significantly, however, it is only Duchenne laughter that has been shown to stimulate endorphin release (Dunbar et al., 2011; Nummenmaa et al., 2016), and there is no reason to believe that non-Duchenne laughter has the same effect, certainly not at the same levels. This means that it was only when voluntary humour emerged in hominins that laughter would have played the role in vocal grooming as proposed by Dunbar. Certainly, situations involving vocal grooming would have provided a good environment to facilitate humorous interaction in adult populations outside of a play situation, despite having involved a lesser degree of arousal. It was possible in such situations that humorous expressions that originated in play could be recalled from memory and repeated in order to stimulate smiling and laughter.

If the role of laughter in a vocal grooming scenario is accepted, it connects Stage 4 with a transition out of the neotenous phase[54] and this correlates with dynamics associated with the role of memory at this stage. Research has shown that adults have superior faculties of memory

[54] Vocal Grooming Theory assumes such grooming to have occurred across all age groups.

retention and recall (Fry & Hale , 1996, 2000)[55]. The conclusions of this research are summed up by Bayliss et al.: "much of cognitive development may represent a cascade in which age-related increases in processing speed mediate most of the developmental increases in working memory capacity" (2003 p.72). This transition meant that humour production would still have required a situation involving positive emotional valence but it was possible for it to occur without requiring the situational element of play, diminishing the importance of arousal and making humour an important component within a broad spectrum of adult hominin social dynamics.

The spreading of humorous behaviour through different age groups would have meant that humour had the potential to become a part of parent/child interactions. An early emergence point for this is implied by the important role that humour has in parent/child interactions in modern humans (Fonagy et al., 2007; Hoika & Ashtar, 2012; Mireault et al., 2012; Reddy, 2001), which often involves a pedagogical element (Esseily et al., 2016; McGhee, 2015) and occurs during the process of postnatal functional cortical development which affects the formation of behavioural patterns (Johnson, 2000; Gao et al., 2009). I cannot find any research indicating the universality of humour in parent/child interactions, but it is proposed that it is reasonable to assume this based on common sense as well as the observed universality of humour (Martin, 2010; Raskin, 2012), high levels of laughter in children (Provine, 2001), the role of humour as a bonding mechanism (Riem et al., 2012; Provine, 2001), numerous studies on humour in child/parent interactions (eg: Hoika & Akhtar, 2012; McGhee, 1979; Reddy, 2001) etc. Such behaviour in the early post-natal phase would have stimulated positive stress modulation, thus positively affecting the epigenetic development of the infant (Franklin et al., 2010; Jawahar et al., 2015)[56]. Humorous behaviour in all ages would also have made humour relevant to mate selection, and this positive correlation in modern humans is well documented (e.g. Bressler & Balshine, 2006; Kaufman et al., 2008; McGhee & Shevlin, 2009). This would have meant that humorous behaviour had the potential to yield substantial new rewards and benefits to hominins, and the related broader mechanism of sexual selection would have ensured that humorous individuals were more likely to reproduce thus replicating any underlying genetic components in succeeding generations.

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[55] This stage of humour was the first one where mature individuals had an advantage over younger individuals in regards to humour production and appreciation.
[56] For a more detailed discussion on the role of humour in a parental context see pp.169-172.

It is proposed that the combination of voluntary control and emergence from the neotenous phase would have accelerated the proliferation of humorous behaviour, due to the increased number of hominins involved, and the effects of enhanced parental care and sexual selection. It is also possible that an increase in the size of social groups may have played a role, regardless whether or not Vocal Grooming Theory is accepted, because humorous behaviour alone (i.e. in the absence of other forms of vocal grooming) was prosocial in nature[57], and furthermore it is possible that it could have served as a communicative method of strengthening social bonds thus, to some degree supplanting physical grooming.

To recap, Stage 4 involved:

1) beginning in early childhood, hominins in situations involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the action(s) of others and/or relating action(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;
2) the use of memory in the production and appreciation of humour, and the consequent yielding of mutual rewards and benefits as a result of memory acquisition, retention and recall;
3) the voluntary control in humour production and the consequent yielding of mutual rewards and benefits as a result of voluntary communication. This included a type of vocal grooming, which promoted social cohesion and served to increase the size of social groups and enhanced the ability of individuals to perceive and regulate emotions in others moving them closer to the point where they would become strategic agentic operators in their own existence as per Social Cognitive Theory;
4) humorous behaviour in all age groups beginning in early childhood. This would have caused humorous behaviour to be associated with rewards relating to mate selection and would also have yielded adaptive benefits related to the broader mechanism of sexual selection. It would also have enhanced parent/infant communication, which would have yielded mutual rewards and benefits, positively affected pedagogical and epigenetic aspects, and had an impact on postnatal functional cortical development;

[57] For a more detailed discussion on the pro-social nature of humour see pp.124-137.

5) the continuance and possible strengthening and broadening of the aspects introduced in preceding stages.

Stage 5 – Repetition from memory by a 2nd party

Summary: driven by rewards, an individual imitated another individual's spontaneous or repeated expression that had stimulated smiling/laughter response(s) on a previous occasion. Just as in Stage 4, the gaps between repetitions would have been small at first. A humorous expression might have been repeated within the same session of play but with a notable gap of time between the two performances. Eventually recall would have occurred in separate episodes of play within the same day, then on separate days etc.

Stage 5 represents an extension the aspect of replication by a second party in Stage 3 in combination with the dynamics outlined in Stage 4. As such, it is representative of both an enhanced level of hominin imitative abilities as well as a mechanism by which such abilities could be further advanced. It was earlier conceded that that the process of replication outlined in Stage 3 might not be considered to qualify as "true imitation", and if Thorpe's criteria[58] are applied (see p.87) it will be seen that true imitation does not occur until a later stage[59]. The dynamics involved in Stage 5, however, show how humorous behaviour would have played a role in the process by which this gap was gradually bridged. As in Stage 4, there would have been rewards (and benefits) yielded by memory retention and recall, and this would have caused the production of humour to gradually become voluntary, but there still remained a connection with instinctive behaviour in that even though the humorous action could be reproduced voluntarily, it was the reproduction of something that was initially created in a more instinctive fashion. The root remained instinctive. The ability to voluntarily replicate the autotelic actions of another in order to yield rewards was an important step in the evolution of the hominin faculty of imitation (which may in turn have contributed to the development of mirror neurons by way of the Baldwin Effect). It would also have greatly broadened the capacity for humorous

[58] Thorpe defines imitation as "the copying of a novel or otherwise improbable act or utterance"

expression and resulted in a further numerical increase in such expressions.

Voluntary control of imitation represented an advance that was quite literally "significant" in that it involved an advance in symbolic competence. By replicating the action(s) of others in a different context (i.e. a different situation) with the intention of eliciting response in common social conspecifics, the action became a symbolic one: it symbolized the initial action. To be more accurate, within Peirce's (1932) classification system[60] the action would be classified as iconic because it resembles what it stands for. When perceived a subsequent time by the same common social conspecifics, this iconic action would have had the potential to trigger the recall of the previously witnessed instances of the same expression(s), inclusive of the previous association with humour/smiling/laughter and other contextual factors, thus potentially stimulating a renewed humorous response and extended meaning. In contrast, if the audience did not consist of common social conspecifics, and the action had never been seen before in a humorous context, then the action would not have been an iconic one for the interpretant(s), only for the interpreter, and as a result, it was the cognitive processing and particulation of constituent elements that was requisite in interpreting humorous content, rather than simple recall. This in turn would tend to lead toward indexical aspects in further interpretations/expressions. In this way we can see the building up of a shared body of social experience and the use of commonly recognized communicative iconic information/expressions to yield mutual rewards. The role of symbolic communication is important to the broader topic at hand and should be given greater consideration once the review of the stages in early humour is complete.

To recap, Stage 5 involved:

1) beginning in early childhood, hominins in situations involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the expression(s) of others and/or relating expression(s) to their body of memories of previous humorous

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[59] Using this definition true imitation would have emerged in Stage 7.
[60] This thesis applies Peirce's classification of signs as interpreted by Deacon in his book "The Symbolic Species"(1997), which proposes the following hierarchy: icon, index, symbol (for more details see p. 139).

experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;

2) the use of commonly recognized communicative icons in the creation and continued development of the shared body of memories of humorous experiences. This represented the development of symbolic competence and shows humorous behaviour to have constituted a system that would have stimulated further evolution of such competence. This process would have yielded mutual rewards and benefits;
3) a continually broadening capacity for humorous expression resulting in a numerical increase in such expressions;
4) the continuance and possible strengthening and broadening of the aspects introduced in preceding stages.

Stage 6 – Accidental variation

Summary: Repetitions and replication of humorous actions produced actions that were **not true copies** of the original (i.e. with some specific observable difference(s)). Some of these variations were humorously successful and thus, continued to be replicated in their evolved form; imitated by others who had the requisite capacity of memory[61].

The increased size of social groups and continually broadening capacity for humorous expression outlined in Stages 4 and 5 would have created larger bodies of socially shared information via humour, numerically increasing the possibility that replication might produce accidental variations incorporating some aspect(s) associated with a second shared humorous expression, thus producing humour through a process of merge[62] where two (humorous) mental

[61] It could be argued that placing accidental variations in Stage 6 is sequentially incorrect: faulty variations may have appeared as early as Stage 3 because the creation of variations would have been an inevitable by-product of the process of replication as is illustrated by Blackmore's statement about emulation "the learner observes another individual gaining some reward and therefore tries to obtain it too, using individual learning in the process, and possibly attaining the goal in quite a different way from the first individual" (2001 p.235). In this type of way, accidental variation may have occurred during Stages 3 – 5, but I have chosen to introduce accidental variation in Stage 6 for the purposes of continuity.

[62] Merge is a term used in linguistics will be discussed later in more detail on the following page (also see p.231).

representations combined to form a third (humorous) mental representation. To illustrate how this might have occurred, consider the following simplified scenario. Imagine a social group of hominins that collectively held 100 different specific expressions in their shared body of humorous experiences ie: primitive clowning. Of these 100 expressions, one was an expression that exaggerated the opening of the eyes and mouth and another involved hopping on one foot. It is would have possible for an individual to merge the two expressions if they were expressed in an overlapping sequence, or due to a fault in memory, or simply because the individual had lost their balance. This would have caused a merging of two comic expressions to form a third comic expression. The two expressions would have remained in the body of shared social experience, but the third merged expression would also have been added to the body of humorous memories. The extended body of 101 humorous memories would then all be potentially subject to the operation of merge on future occasions (i.e. the process was a recursive one) and included this novel expression that constituted more than the sum of its parts because the unexpected merging of the two events would have created an additional incongruity.

The incongruous merging of elements (e.g. anthropomorphizing, the merging of the human and the non-human[63]) has been noted to be a common comic tool (eg: Critchley, 2011; Lavery, 2005; Molineux, 2014; Wardenaar, 1975) and I have often seen it applied in Stand-up Comedy and Improvisation as well as in children's mix/match or cris/cross jokes (eg: Q: What do you get when you cross a cow with a trampoline? A: A milkshake!). Even though this is a linguistically based example that involves much greater complexity than the humour under consideration, it is representative of a simpler root involving merge, which is expressed in other forms of childhood humour (McGhee, 1979). It is also notable that events involving novel instances of merge fit comfortably into the framework of incongruity theory, indeed they can be seen as the essence of them.

Despite the apparent simplicity of the process of merge as described, the emergence and proliferation of voluntary expressions involving recursive merge had broader implications in

[63] It is also notable that anthropomorphic blending necessarily involves the volitional cross-comparison of the notions of self and other and would have contributed the evolutionary conscious emergence of such notions. The prevalence of such types of humour is a remnant of the psychological importance of this process.

terms of the evolution of hominin cognition and the emergence of language[64]. In linguistic terms Chomsky defined merge as "an indispensable operation of a recursive system ... which takes two syntactic objects A and B and forms the new object G={A,B}" (1999 p.2). In this case the merge described involves two "syntactic objects", which makes it appear to be a more complex operation as is illustrated by the following passage describing syntax objects:

> (t)he input and output of a macro transformer (i.e. source and replacement forms) are represented as syntax objects. A syntax object contains symbols, lists, and constant values (such as numbers) that essentially correspond to the quoted form of the expression. For example, a representation of the expression (+ 1 2) contains the symbol '+ and the numbers 1 and 2, all in a list. In addition to this quoted content, a syntax object associates source-location and lexical-binding information with each part of the form (source: racket-lang.org).

The apparent complexity of the notion of syntactic objects, however, does nothing to diminish the fact that the general operation of recursive merge is common to both language and simple forms of humour. It is the essential process of recursive merge that is of prime importance rather than the simple or complex nature of that which is being merged. In relation to hominin humour, merge applied to mental representations[65] (for a review of mental representations see Jackendoff, 1995), and the role of humour in the merging or blending of mental representations was noted by Koestler in his book, The Act of Creation (1964), in which he referred to the process as the "bisociation of matrices". Fauconnier and Turner cited the notion of the bisociation of matrices as important in developing their Conceptual Integration Theory (2008) where they employ the term "conceptual blending". They describe the process as follows: "In blending structure from two input spaces is projected to a separate space, the 'blend'. The blend inherits partial structure from the input spaces, and has emergent structure of its own." (1996, p.130). Further to this, conceptual blending has been noted to be an element in humour (Coulson, 2001, 2005)[66]. It could also be argued that all humour appreciation based on incongruity involves merge (or bisociation or blending) as per Koestler's ideas (1964), within the

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[64] As was mentioned earlier, autocatalysis is necessarily recursive in its nature.
[65] Mental representation is the mental imagery of things that are not actually present to the senses. (McKellar, 1957).
[66] Also see Wang & Lin (2003) and Dynel (2011).

process of cognitive cross-correlation. In relation to simple hominin humour, an expression is cognitively processed, it violates expectation(s) and humour results. As such there is the perceived expression (a), the mental representation of the associated norm(s) (b), and the comic conception (c): a merges with b to produce c. As such, it can be seen that hominin humorous behaviour involved the merging of mental representations and associated rewards and benefits would have served to promote the capacity for this, which would have advanced cognitive abilities that would have been central in the emergence of language.

Returning to the notion of accidental variation, memory recall is often subject to errors (Cramer, 1972; Eisenhower et al., 1991) and it has been shown that false memories are more likely to be produced during positive mental states, possibly due to the engagement of relational processing (Storbeck & Clore, 2005): memory recall includes related material that was not actually part of the remembered experience. This implies that humorous expressions would have been prone to accidental variation. Testing of this type of memory error is typically language based (e.g. the Deese-Roediger-McDermott paradigm (Watson et al., 2004)), but this is simply because language provides a convenient and efficient frame of reference to apply research to. Language serves to provide discrete elements that are configured to represent information derived from multiple mental schemata. In a pre-linguistic scenario humour would have involved similar dynamics in relation to schemata but would have had a lower level of complexity related to the organization of discrete elements. The term schema is being used here to refer to organized blocks of mental representations, and schemata can be thought of as per Wadsworth (1996) as 'index cards' filed in the brain, which help to determine responses to incoming stimuli or information. The term “schema” also incorporates the behaviour associated with cognitive aspects as is reflected in Piaget et al’s description of a schema as: "a cohesive, repeatable action sequence possessing component actions that are tightly interconnected and governed by a core meaning." (1952, p.240). The use of these terms should not be construed as an endorsement or refutation of any particular approach to cognition and behaviour, these are simply terms that are well established in related academic discourse (Tse et al., 2007) and the notion of considering humour in relation to schemata has been proposed by various researchers (eg: Honeycutt & Brown, 1998; Snell, 2006; Tsoi et al., 2008).

In neurological terms schemata can be seen to manifest themselves as pre-existing networks of interconnected neocortical representations, but this should be seen only as an analog because the notion of an actual neural schema is more complex and problematic (eg: Dodge & Lakoff,

2005; Mackenzie et al., 2014). Such pre-existing networks of interconnected neocortical representations serve to enhance the consolidation of memory (Morris, 2006, van Kesteren et al., 2012), which is relevant to the evolutionary phase under consideration. It is notable that novelty has also been seen to enhance the consolidation of memory (Adcock et al. 2006; van Kesteren et al., 2012; Nyberg, 2005), and there is a substantial degree of overlap between the notions of novelty and incongruity (eg: Berlyne, 1972; Caron, 2002; Forabosco, 2008). As such, humorous behaviour would have served to consolidate memories, and these memories were more likely to be subject to errors due to false recall in humorous situations.

Within Stage 6 it was also possible for some accidental variations to have created a symbolic element. Returning to the specific example of humorous merge that was given earlier, hopping on one foot was one of the expressions within shared body of humorous experiences, and simply standing on one foot might have the potential to recall the humorous experience of hopping on one foot due its essential similarities. As such, this partial representation reduced the original action to a specific symbolic element: standing on one foot: an index, as per Peirce's definition (1932), of the original humorous event. This form of communicative shorthand was similar to repeating a punch line in order to recall a joke and if the expressions was recalled and repeated at a later point it would have represented voluntary use of symbolic communication in hominins.

To recap, Stage 6 involved:

1) beginning in early childhood, hominins in situations involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the expression(s) of others and/or relating expression(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;
2) the accidental creation and continued development of commonly recognized communicative indices caused by reductive errors in memory recall, the use of which yielded mutual rewards and benefits;
3) the accidental creation of humour involving the operation of merge caused by relational errors in memory recall, the likelihood of which was increased by the affective state of humour. The expression of these merged communicative forms

would have yielded mutual rewards and benefits and have constituted an advance in hominin cognitive capacities specifically relevant to the emergence of language;

4) the continuance and possible strengthening and broadening of the aspects introduced in preceding stages.

Stage 7 – Combination and reconfiguration

Summary: the increased use of various combinations of icons and indices drawn from the body of humorous memories led to the volitional creation of novel humorous events involving the manipulating of mental representations held in multiple schemata. This process was stimulated by rewards, and yielded adaptive benefits that enhanced the chances that any related genetic aspects would be passed on to successive generations.

It is reasonable to believe that hominins had the cognitive potential for Stage 7 based on the learning abilities (Reader & Laland, 2002; Tagliatela et al., 2012) and limited capacity for symbolic communication (e.g. Miles, 1983, 1999; Savage-Rumbaugh et al., 1985) observable in apes, and the fact that apes have some degree of voluntary control of gestures, facial expressions, and to a lesser extent, vocalizations (Hopkins et al., 2011; Pollick & De Waal, 2007). In addition to this evidence, the accumulation of the various positive effects of humorous behaviour that have already been mentioned in regard to hominin cognitive evolution and social learning would also have a played a contributing role.

In Stage 7 the body of humorous memories in hominins would have been expanded, further integrated, and would have become subject to voluntary recall and reconfiguration. As such, it is more accurate to use the term schema rather than “body of humorous memories” because of the increase in operational elements stimulated by volitional humour and the use of symbolic expression within such humour. Put simply, there was not only a store of knowledge but also information about how this knowledge could be used (as per Rumelhart, 1980). This use of the term schema corresponds with the Piagetian behavioural aspect of the term that was mentioned earlier and is in agreement with the notion of a “humour schema” as proposed by other scholars (eg: Honeycutt & Brown, 1998; Tsoi et al., 2008). A comprehensive review of existing schema theories would not be of value within this thesis, so I will simply apply Ghosh and Gilboa’s model (2014) in order to provide necessary framing and explanation. Within their model, Stage 6 would have involved three of the four proscribed schema features:

i) an associative network structure i.e. specific units [67] (that can be considered as elements, events, features, or variables) and their interrelationship: “without units, a schema could not hold any information, and without their interrelations, that information would be isolated and its meaning vastly restricted” (Ghosh & Gilboa, 2014 p.106). Percieved incongruity in the patterns related to such units and their interrelations that would have provided the cognitive raw material for humour;

ii) basis on multiple episodes: “extracted commonalities from multiple episodes form a cohesive collection of inferences about the possible occurences of a set of events or objects within the context of the schema” (Ghosh & Gilboa, 2014 p.106) . Multiple episodes are necessary in order to create the patterns in memory/expectation that are then violated in instances of humour;

iii) a lack of unit detail: “a lack of detail follows directly from their basis on multiple episodes, since no two episodes are identical” (Ghosh & Gilboa, 2014 p.106).

Stage 7 would also have involved adaptability, the fourth proscribed feature. Adaptability refers to the capacity for modifications of the schema as a result of new sensory input and this capacity is significant because it involves the ability “to store vast amounts of information derived from many experiences and update that information” (Ghosh & Gilboa, 2014 p.108)[68].

The recall and reconfiguration of mental representations retained in multiple schemata would have contributed to the creation of novel humorous behaviour in numerous different ways including but not limited to: sequences, merge, the reductive isolation of a specific action or actions (involving the creation of indices), repetition, and/or combinations of any of the preceding. Put simply, variations in perception of patterns in relation to intrinsic aspects such as those just listed, or extrinsic aspects (i.e. context) had the potential to produce humour. The

[67] It is possible to interpret ent such reductionist “units” as symbolic and as such, volitional humour production can be seen as symbolic in nature.

[68] It is also proposed that Stage 7 would have marked the beginning of the gradual emergence of four additional features that schemas are sensitive to: chronological relationships, hierarchical organization, cross-connectivity, and embedded response options (for an overview of these features see Ghosh & Gilboa, 2014). Spatial limitations make it impossible to devote analysis to these at this point.

perceived novelty of patterns would have played a role in determining the level of incongruity and thus, the level of rewards and adaptive benefits that might be yielded. Greater novelty was roughly equivalent to greater humorous incongruity, which would generally produce greater response. It is acknowledged that this correlation was not necessarily 1:1 and there was the possibility of more complex dynamics as per theories regarding arousal jags (Berlyne, 1972, Rothbart, 1977)(Berlyne describes arousal jags as "slight and transitory jumps in arousal become pleasurable as a consequence of the drop in arousal that quickly terminate them"), but in general terms, the positive correlation would have been present. The basic idea being that moderate novelty is ideal and beyond a certain threshold increased novelty does not translate into increased humour. It is proposed that the dynamic of greater novelty in reconfiguration yielded greater reward, stimulating the development of a higher level of flexibility in associated cognitive operations thus creating more advanced cognitive abilities and a pre-disposition towards novel syntheses within the humour schema: reward for the creation of novelty stimulated further creation of novelty and this would have been manifested in neurological as well as behavioural terms.

Stage 7 would have involved both the voluntary creation of novel humorous actions and the true imitation of those actions. It was already outlined how from Stage 3 onwards, humorous behaviour would have promoted and accelerated the evolution of imitative/pre-imitative behaviour. By Stage 7 this process reached to the point where hominins were capable of true imitation as defined by Thorpe (see p.87). The implications of the acceleration of the imitative capacity and its domain-general proliferation in hominin populations is broadly significant and a brief summary of some the more relevant aspects of imitation will now be provided.

Imitation is innate in humans (Butterworth, 1999; Meltzoff & Decety, 2003) and is an extraordinary act in that it involves the creation of shared neural representations between the self and the other(s): mutual neural activity occurs as the result of social behaviour without any requisite physical cause and effect. This process of shared neural representations involves distinguishing between the perspectives of self and other (Meltzoff & Decety, 2003), which is relevant to Theory of Mind (Meltzoff & Gopnik, 1993). It is worth noting that in their study of imitation and memory in infancy Meltzoff and Moore (1977) noted that the most commonly imitated facial expression observed over a 15-year period was tongue protrusion. Oddly enough, unlike Einstein they failed to note tongue protrusion as being a humorous act, and somewhat ironically they ask "(w)hat would motivate an infant to imitate yesterday's observed

behavior?" (2002, p.58). The answer they propose is that infants use imitation to reidentify an individual, but this relates to function rather than motivation. The rewards yielded by humour can be seen to provide the correct answer in this instance. From a cognitive perspective, imitation has been seen to enhance memory, particularly when it involves novel (i.e. incongruous) input (Meltzoff, 1988). As such, the use of true imitation in humorous behaviour would have further strengthened humour's potential to stimulate/reward acts involving memory, and the yielding of adaptive benefits would have served to replicate any underlying genetic aspects in succeeding generations.

From a social/behavioural standpoint, humour-stimulated imitation would have enhanced the process of social learning and as such, humour can be seen as a pro-memetic mechanism. A meme is any idea, behaviour or trend that has the ability to transmit from person to person (Dawkins, 1976). The notion of memes is somewhat contentious (e.g. Benitez-Bribiesca, 2001; Bloch, 2000), but a comprehensive discussion on the points of contention is not of value within this thesis. In relation to the notion of social learning, social learning can be seen to be a system of information transmission while a meme is a specific component within such a system. So for those who endorse the notion of memes, memetic behaviour represents a specific form or mechanism of social learning. The social learning and memetic behaviour that is observable in humans differs from social learning and "imitative" behaviour in animals in that it is ubiquitous and domain-general (i.e. it does not rely on drives relating to fear, food or sex). Blackmore makes a further clarification in relation to memetic behaviour by stating it involves the transmission of novel behaviours from one individual to another rather than the mere application of an innate behaviour in a novel situation (2000). From an evolutionary perspective, the primary question regarding imitation is why did the imitative faculty become so developed in hominins? It is not feasible to propose that this occurred due to adaptive benefits relating to food acquisition, mate selection etc., that were conferred by imitative behaviour because human imitative behaviour is domain-general. If it evolved as a domain-specific mechanism it would have remained domain-specific. It is proposed that humorous behaviour served to create a domain-general framework for imitative expression. As such, in hominin groups humour was equivalent to a game that "culturally evolved for the 'purpose' of expanding the range of action units that

children can imitate" (Heyes, 2016 p.4)[69], though this was not its only "purpose". As such, it is possible to see humour as having been a powerful influence in the emergence of ubiquitous domain-general imitative (i.e. memetic) behaviour.

Hurley et al. speculated on the relationship between memes and humour in their book "Inside Jokes", referring to jokes as "memes evolved for enjoyment" (2011 p.214). In their discussion on humorous memes they state "these quasi-independent informational entities can foster their own replication...independently of any fitness advantage they specifically offer to their hosts" (2011 p.291-2). While I am not in agreement with their use of language, which presents memes as individual volitional entities able to "foster their own replication", I do agree with the idea that the humour-driven evolution of systems to share information with social conspecifics changed the nature of evolutionary dynamics. The social learning that would have occurred in conjunction with memetic behaviour constituted a specific mechanism capable of influencing behavioral phenotypic variation and would have resulted in socially oriented adaptive dynamics, which differed from more strictly biologically determined ones. In this scenario, an individual's "fitness" level was no longer purely biologically determined and within the proposed model, humorous behaviour helped to bridge the gap between the biological and the biosocial.

Regardless of the potential implications of the emergence of imitative behaviour, the process of imitation in humorous behaviour is clearly demonstrated by the four distinct processes that memes go through as proposed by Heylighen and Chielens (2008): assimilation (by an individual who becomes the carrier or "host" of the meme), retention (within memory), expression (through an action or any other means that can be perceived by others), and transmission (to one or more individual(s)). Furthermore, humour at this stage involved the four prerequisites for learning proposed by Miller and Dollard (1941)(drives, cues, responses, and rewards)[70] and because the drives were created by the rewards, a positive feedback loop was engaged enabling it to function in an autocatalytic manner. So within the proposed model it can be seen that the emergence of humour introduced an autocatalytic system involving social

[69] For more on this see pp.87-88.
[70] Put simply, **drive** stimulus impels **responses** which are typically modified by **cues** derived from other stimuli, and these responses have the potential to yield **reward**. For further clarification see Miller & Dollard, 1941 p.30) for example, hunger is the drive and food is the reward, whereas in humour the promise of laughter is the drive and laughter etc. is the reward. it is also possible to see "rewards" in this context as including benefits

learning and the creation and transmission of domain-general information (memetic or otherwise).

Stage 7 was also remarkable because it introduced individual creativity into hominin communication. For the first time, hominin individuals could voluntarily create novel expressions that would have led to the creation/expansion/alteration of bodies of commonly held mental representations related to multiple schemata within social groups. Humorous behaviour at this point involved the organization and sharing of mental representations, i.e. domain-general social learning. Information within humorous expressions would have incorporated both icons and indices, and the element of novelty would have enhanced the processes of memory acquisition, retention and recall. Rewards yielded by humorous behaviour would have stimulated/facilitated further novel behaviours (humorous or otherwise) and this would have resulted in more active, complex and flexible cognitive dynamics in regards to the cross-correlation of information between schemata, including their particulated indexical and iconic constituents. From a behavioural perspective, the dynamic created by the combination of voluntary creative communication and the reward for novelty would have stimulated behaviours that would have differentiated an individual from their social conspecifics. As a result of this, voluntary individualism would have yielded rewards and benefits. This represented the introduction of voluntary control of the presentation of self as well as the differentiation between self and others, which is the hinge-pin to the notion of Theory of Mind.

To recap, Stage 7 involved:

1) beginning in early childhood, hominins in situations involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the expression(s) of others and/or relating expression(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits;
2) the continued expansion and integration of the schema of humour, which became subject to voluntary recall and reconfiguration. This process would have yielded mutual rewards and benefits;
3) greater potential for novelty in reconfiguration, with increased novelty yielding greater rewards and benefits, and improving future memory recall of the humorous action in question;

4) the use of true imitation, which effected domain-general memetic behaviour and resulted in an increase in the potential for social learning. This behaviour would have yielded mutual rewards and benefits. The presence of true imitation was indicative of the continued development of Theory of Mind;
5) the introduction of creativity into hominin communication resulting in more active, complex and flexible dynamics relating to the associated schemata including their indexical and iconic constituents. This process would have yielded mutual rewards and benefits;
6) an increase in novel and individualistic behaviour, which stimulated the development of Theory of Mind as well as yielding mutual rewards and benefits;
7) the continuance and possible strengthening and broadening of the aspects introduced in preceding stages.

Stage 8 - Ideation

Summary: novel actions were ideated and performed with the voluntary intention of stimulating smiling/laughter spectrum responses. Initially these would have been in some way associated with previously experienced humorous actions and/or their specific elements but would have become increasingly independent. This process was stimulated by associated rewards, and any related genetic aspects would have been subject to improved chances of replication due to associated adaptive benefits.

Put simply, Stage 8 was the point at which hominins were first able to ideate and express novel humorous actions: to create humour “from scratch”. While novel humour was created in Stage 7, its constituents were all drawn from the body of shared mental representations relating to humour within the humour schema. As such, the potential operations of humour were potentially broad, but still finite. Stage 8 would have involved the processing of both exteroceptive and interoceptive information from outside the humour schema in order to ideate humorous actions that were subsequently expressed. It is reasonable to assume this step to have been possible due to the advanced general level of cognition and social organization attributable to hominins at the evolutionary period under consideration (relative to other species) as well as the

generative, cumulative effect of the operation of humour in Stages 1 through 7[71]. The integration of general exteroceptive and interoceptive information in the creation of humour meant that the potential for humour creation was now infinite, even though the number of humorous mechanisms involved in expression (i.e. repetition, exaggeration etc.) was limited. As such, humour at Stage 8 represented a cognitive/communicative system where finite mechanisms (i.e. humorous devices such as repetition, exaggeration etc.) had the potential to create an infinite number of expressions.

The creation of humour from exteroceptive and interoceptive information that was (at least partially) separate from the humour schema, would have involved the voluntary, cognitive cross-correlation and reconfiguration of information from multiple schemata in order to process the level of incongruity between elements of the information and the strength of associations between the information and information within the humour schema. It also would have involved the expression of the resulting reconfigurations, which thus would have been shared with social conspecifics. This was an informatic process involving abstracted incongruities, which contributed to development of the humour schema as well as any other involved mental schemata. Furthermore it was a communicative process that would have shared any such development in schemata within social groups and yielded rewards and adaptive benefits for such sharing. Essentially, for a hominin individual, by Stage 8, mental representations could be interpreted through the lens of the humour schema, arranged accordingly, and shared with others. This represented a very simple cognitive mechanism for organizing and sharing information. It is proposed that this process of organizing and sharing information through humour marked the emergence of the hominin capacity for voluntary cross-correlation of particulated mental information between multiple schemata. As such, hominin cognition became an integrated, partially voluntary system involving specific, cross-correlated schemata using common discrete elements (i.e. icons, indices, etc.) that was shared between social conspecifics. This was also a cumulative, hierarchical process constituting the "self-embedding

[71] It is stressed that humour's role in cognitive evolution would not have existed in isolation from other cognitive/behavioural aspects of hominins such as tool use (e.g. Morgan et al., 2015; Toth & Schick, 1993), hunting practices (e.g. Stanford, 1996), and a variety of social/behavioural aspects (eg: Donald, 1991; Flinn et al., 2005). The proposed role of humour should be considered as an addition to these and other factors but the comprehensive consideration of such interrelationships is not possible dues to the limited space available within this thesis.

hierarchical structure in cognition" described by Matsuzawa (2008 p.3)[72], and thus marked an acceleration in the rate of hominin cognitive evolution.

This position invites comparison with theories involving modularity of mind (e.g. Carruthers, 2006; Fodor, 1983) domain-specificity (e.g. Cosmides & Tooby, 1994; Leslie, 1994), and connectionism[73] (e.g. Flusberg & McClelland, 2014; Smolensky, 1988), but a comprehensive discussion on these topics, while interesting, would not be productive in relation to the topic(s) under consideration. I will, however clarify that I have chosen to use the term "schema" rather than "domain" partly in order to avoid confusion with the domains referred to in the term "domain-general". The term domain-general within this thesis refers to the full, unrestricted range of an individual's cognitive/perceptual input and/or behavioural environment (as opposed to specific domains such as mate selection or food acquisition) and does not refer to mental representations and/or their related neurological aspects. Bearing this in mind, the proposed notion of a transformation from a flow of information to a complex shared organization and hierarchical interrelation between discrete elements can be related to Mithen's notion of "Cognitive Fluidity" (1996)[74].

On an interesting side note, by Stage 8 it is also reasonable to attribute the faculty of consciousness to hominins due to the presence of voluntary cross-correlation of information between schemata and the reconfiguration and communication of such information. The nature and origins of consciousness are vast and nebulous subjects and Ned Block is quite correct when he says that consciousness is "a mongrel concept: the word 'consciousness' connotes a number of different concepts and denotes a number of different phenomena" (Block, 1995 p.1). I will not explore this subject in any depth but I will make a few brief relevant observations with apologies for the necessary degree of précis as this topic is worthy of an entire doctoral thesis. The proposed model has already introduced a number of factors such as Theory of Mind and

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[72] Matsuzawa states "it is possible to pinpoint the main difference between human and chimpanzee intelligence as lying merely in the depth of hierarchical levels" (2008, p.3).

[73] Flusberg and McClelland define Connectionism as "a computational modeling framework inspired by the principles of information processing that characterize biological neural systems, which rely on collections of simple processing units linked together into networks. These units communicate in parallel via connections of varying strength that can be modified by experience" (2014, p.1).

[74] Mithen describes "Cognitive Fluidity" as representing "when thoughts originating in different domains can engage together" (1996 p. 77).

Joint Attention that figure prominently in many theories regarding the origins and nature of consciousness (e.g. Donald, 2001; Humphrey, 1999). In discussing the origins of consciousness, Panksepp describes the self as a "neural 'stage manager' who does not observe, but rather, has the ability to generate various coherent acts in response to archetypal survival challenges" (1998, p.568). The "self" as described by Panksepp was clearly present in Stage 8 and the evolutionary steps to that point have been outlined. There was, however, one difference in that the motivation was not archetypal survival challenges but the promise of rewards. Returning to Block, the cross-correlation between schemata and related behaviour that has been outlined as occurring during humour can be seen to represent the "broadcast for free use in reasoning and for direct "rational" control of action" (1995 p.5) he describes in his definition of access consciousness: Stage 8 humour involved the volitional organization of abstracted information and the modification of behaviour based upon this organization. The definition of consciousness that is perhaps most directly connected with the proposed model is that of the ethologist John Crooks: "Conscious awareness is a conditional property of the reality model in its tripartite form. It may be said to be the subjective aspect of the continuing re-presentation of a temporarily stabilized informational display within which multilateral processing of an issue can occur" (Crooks, 1987 as quoted in Humphrey, 1999 p.34). Within the proposed model, hominins creating volitional humour can be seen to have been subjectively re-presenting a temporarily stabilized informational display involving multilateral processing and in this way demonstrated themselves to be fully conscious agents. It cannot be definitively stated that the emergence of humour specifically stimulated the emergence of conscious awareness, but it is proposed that further research and theorizing on this idea is merited.

Returning to the more general consideration of Stage 8, it would have involved individuals ideating and expressing humour, and the potential for reward was predicated on two factors: 1) whether or not the expression broke a pattern (or patterns) of expectation of the observer(s) and 2) whether or not the observer(s) associated the expression with information within their humour schema. Thus, the ability to predict which expressions would be successful in these regards would have resulted in a greater yield of mutual rewards and adaptive benefits. As such, humorous behaviour would have served to facilitate the evolution of several higher level cognitive processes because it involved thinking about thinking (metacognition), thinking about someone else's thinking (i.e. Theory of Mind), as well as direct rational control of thought and action (i.e. access consciousness). The significance of this can be illustrated by the fact that

Dunbar et al.'s (2016) description of the mentalizing competences involved in language applies equally to humorous interactions in Stage 8:

> Language requires considerable mentalizing competences on the part of both speaker and listener: the speaker has to intend that the listener understands that he/she intends to convey something, and the listener reciprocally has to understand that the speaker intends the listener to understand something[75] (Dunbar 1998; Sperber and Wilson 1995). In effect, a conversational exchange minimally requires third-order mentalizing (i.e. the representation of three embedded mindstates) (p.131).

The following summary of Stage 8 will include a summary of all the factors that have been cited in Stages 1 through 8 in order to emphasize the hierarchical evolutionary process as well as the totality of ramifications of the emergence of humour during its early stages. To recap, Stage 8 involved:

1) beginning in early childhood, hominins in situations involving positive emotional valence, perceiving a specific incongruity (or incongruities) in the expression(s) of others and/or relating expression(s) to their body of memories of previous humorous experiences and producing a smiling and/or laughter response. This process would have yielded mutual rewards and benefits, which would have fostered the ability to detect breaks in expected patterns of perception and strengthened the association between breaks in expected patterns of perception and a positive emotional state;
2) the voluntary intentional processing of potentially infinite exteroceptive and interoceptive information separate from the humour schema in conjunction with information within the schema to ideate novel humorous actions that were subsequently shared with others. As such, humour represented a cognitive/communicative system where finite mechanisms had the potential to create an infinite number of expressions i.e. there was recursive merge operating within an infinite framework. This process would have yielded mutual rewards and benefits;
3) the voluntary, intentional cross-correlation of information between multiple schemata involving the use of mental representations, including icons and indices held in

[75] Arguably, humour represents a simpler transitional phase because it requires only perception rather than understanding on the part of the "listener".

common between schemata and within specific social groups. This represented an advance in symbolic competence and constituted the operation of conscious awareness as per numerous definitions (e.g. Block, 1995; Panksepp, 1998; Crooks, 1987 etc.). This process would have yielded mutual rewards and benefits;

4) the act of predicting what others would find funny, which required social meta-cognition (Theory of Mind): thinking about another individuals thinking. This involved direct rational control of thought and action and would have yielded mutual rewards and benefits thus fostering the evolutionary development of this faculty;
5) the continuance and possible strengthening/broadening of the aspects introduced in preceding stages including:
    i) the continued expansion and integration of the schema of humour, which became subject to voluntary recall and reconfiguration and this process would have yielded mutual rewards and benefits;
    ii) greater potential for novelty in reconfiguration, with increased novelty yielding greater rewards and benefits, and improving future memory recall of the humorous action in question;
    iii) the use of true imitation, which effected domain-general memetic behaviour and resulted in an increase in the potential for social learning and this behaviour would have yielded mutual rewards and benefits (the presence of true imitation was also indicative of the continued development of Theory of Mind);
    iv) the introduction of creativity into hominin communication resulting in more active, complex and flexible dynamics relating to the associated schemata including their indexical and iconic constituents and this process yielded mutual rewards and benefits thus fostering the evolutionary development of this faculty;
    v) an increase in novel and individualistic behaviour, which stimulated the development of Theory of Mind as well as yielding mutual rewards and benefits thus fostering the evolutionary development of these faculties;
    vi) the accidental creation and continued development of commonly recognized communicative indices caused by reductive errors in memory recall, the use of which yielded mutual rewards and benefits thus fostering the evolutionary development of this faculty;
    vii) the accidental creation of humour involving the operation of merge caused by relational errors in memory recall, the likelihood of which was increased by the affective state of humour and the expression of these merged communicative

forms would have yielded mutual rewards and benefits and have constituted an advance in hominin cognitive capacities specifically relevant to the emergence of language;

viii) the use of commonly recognized communicative icons in the creation and continued development of the shared body of memories of humorous experiences and this represented the development of symbolic competence and shows humorous behaviour to have constituted a system that would have stimulated further evolution of such competence, which would have facilitated the emergence of language (this process yielded mutual rewards and benefits);

ix) a continually broadening capacity for humorous expression resulting in a numerical increase in such expressions;

x) the use of memory in the production and appreciation of humour, and the consequent yielding of mutual rewards and benefits as a result of memory acquisition, retention and recall thus fostering the evolutionary development of these faculties;

xi) the voluntary control in humour production and the consequent yielding of mutual rewards and benefits as a result of voluntary communication (this included vocal grooming, which promoted social cohesion and served to increase the size of social groups and enhanced the ability of individuals to perceive and regulate emotions in others ~~and~~ moving them closer to the point where they would become strategic agentic operators in their own existence as per Social Cognitive Theory);

xii) humorous behaviour in all age groups beginning in early childhood and this would have caused humorous behaviour to be associated with rewards relating to mate selection and would also have yielded adaptive benefits related to the broader mechanism of sexual selection as well as enhanced parent/infant communication, which would have yielded mutual rewards and benefits, positively affected pedagogical and epigenetic aspects, and had an impact on postnatal functional cortical development;

xiii) the use of pre-imitative/imitative behaviour and the association of this behaviour with mutual rewards and benefits thus fostering the evolutionary development of this faculty;

xiv) the creation, within specific social groups, of a shared body of memories of humorous experiences;

xv) engagement in acts involving repetition and joint attention, which facilitated social learning and advanced the development of Theory of Mind and this process would have yielded mutual rewards and benefits thus fostering the evolutionary development of this faculty;

xvi) the synchronous experience of antiphonal laughter, which enhanced the potential of existing rewards and benefits, and added to them improved social memory and enhanced perceptual sensitivity to the actions of others, which in turn increased their success in subsequent joint-action tasks;

xvii) enhancement of the ability to detect breaks in expected patterns of perception and strengthening of the association between breaks in expected patterns of perception and a positive emotional state.

I thank the reader for their patience with the methodological practice of showing the full summary of each stage but it is hoped that this has served to emphasize the cumulative, generative, and hierarchical nature of the process by which humour may have emerged. Stage 8 does not represent the end of the evolution of humour, but it does represent a clear end-point at which it can be said that the process of emergence concluded, which makes it possible to now consider the ramifications of the use of humour.

8 Ramifications of the general use of humour

Having outlined the specific causal sequence involved in the emergence and initial evolution of humour in hominins, it is valuable to put this information in broader context: hominins could produce and appreciate humour, but how was that important in evolutionary terms, and how did this early humour manifest itself? Based on studies of play in apes (e.g. Pellegrini & Smith, 2005[76]; Ramsay & McGrew, 2005; Vauclair & Bard, 1983[77]), it is reasonable to believe that early humorous behaviour in hominins would have involved body movements, facial expressions, the

[76] Pelgrini and Smith state "play during animals' juvenile period, or period of immaturity, was "critical" in shaping later development. This notion of the deferred importance of juvenile play for subsequent development was later incorporated into Piaget's (1962) and Vygotsky's (1967) theories of play in human development"

[77] Vauclair and Bard focus primarily on the manipulation of objects.

manipulation of objects, and the creation of sound through vocalizations and actions with or without the use of external objects. As such, humorous expressions would have had a physiological component for those creating them as well as for those who experienced laughter/smiling responses. From a cognitive standpoint, the operation of humour would have involved a humour schema which would have cross-correlated and reconfigured extrinsic information derived from perceptual information and intrinsic information derived from multiple schemata in order to create humorous expressions. Humorous expressions would have served to share informatically processed information utilizing icons and indices between social conspecifics creating shared bodies of information. For example, an individual could create a humorous expression by pretending to eat a stone (similar to Chaplin eating a shoe in the 1935 film "The Gold Rush"), the incongruity involved would have shared the actual expression but also the implicit idea of the stone as "non-food" and this in turn, served to provide knowledge that would have helped to develop the idea of "food" as an abstract concept. Essentially, humour functioned as a "break-in-pattern" recognition system, and by recognizing breaks in patterns it became possible to recognize the patterns themselves, and such information was simultaneously shared within the group[78]. Rewards helped to perpetuate humorous behaviour, while adaptive benefits helped to sustain it in the long run by favouring the phenotypic variation of humour and passing on any related genetic aspects to succeeding generations. Before extrapolating any further on the possible ramifications of general humorous behaviour in hominin populations it is first necessary to briefly clarify some of the terminology and ideas related to humour and cognition. Humour is often thought of merely as a type of behaviour, but in an evolutionary context, its cognitive aspects are of equal importance and need to be clearly understood and placed within a behavioural context.

8.1 Cognitive elements

Schemata, domains and modules

The term schema has already been defined and discussed but it needs also to be understood in relation to domains and modules; the following is a brief overview of the subject. Modules and

[78] Humour also functioned directly as a pattern recognition system due to the operation of humorous recall.

domains are terms most associated with evolutionary psychology (eg: Cosmides & Tooby, 1994; Samuels, 2000) but are also applied in the fields of childhood development (Karmiloff-Smith, 1995; Demetriou and Kazi, 2013), linguistics (Fodor, 1983; Van de Lely, 1997) and other areas of cognitive science (eg: Hirschfeld & Gelman; Peretz & Coltheart, 2003). It has been theorized that the human mind has different mental modules, intelligences, or cognitive domains, each of which is associated with a specific area of behaviour (Fodor, 1983). A module or domain can be defined as "a specialized, encapsulated mental organ that has evolved to handle specific information types" (Bates, 1993 p.136) though there are different interpretations, as well as related notions of innateness, localization, and domain-specificity, (for an overview see Bates, 1993).

The term schema has been adopted in regard to cognition in this thesis, rather than module or domain, for two reasons. Firstly, the term schema has often been framed in a way that is inclusive of behavioural aspects (eg: Piaget, 1971) and is not limited to cognition. As such, schema is a more flexible term for the task at hand, though with minor modifications, the terms domain and/or module could often be considered interchangeable[79]. The second reason is that the term "domain" is also commonly applied in a looser sense in relation to extrinsic elements relating to behaviour (eg: Francis et al., 2012; Holtman et al., 2007) and/or environment (eg: Baldanzi et al., 2013). It is more expeditious to restrict use of the term "domain" to this extrinsic sense within this thesis, but it will still be necessary to occasionally make some distinction between intrinsic domains (i.e. cognitive domains) and extrinsic domains (i.e. behavioural/environmental domains). It is also acknowledged that the distinction between intrinsic and extrinsic domains is somewhat illusory in that intrinsic and extrinsic domains are interrelated notions. For example, if a particular behaviour is engaged in consistently, the corresponding cognitive activity can be said to represent a specific domain. This is well illustrated by De Groot's (1978) research that showed expert chess players could only remember the positions of pieces better than novices if the pieces were arranged in a meaningful configuration. This was seen as an example of domain-specific knowledge, and as such the associated cognitive processes were considered to be an intrinsic, cognitive domain. In

[79] As was stated earlier, while specific neural activity related to humour processing will be discussed, there will be no attempt made to speculate on or to map a specific neural humour schema (or domain/module).

sum, the designations of intrinsic and extrinsic are merely convenient shorthand in presenting a clear picture of a complex subject.

Domain-generality and domain-specificity

While an intrinsic domain is considered to be an encapsulated mental organ, it has been proposed by numerous researchers that intrinsic domains do not exist independently (Gardner, 2011; Karmiloff-Smith, 1992; Mithen, 1996) and that "one typically encounters complexes of the intelligences functioning together smoothly, even seamlessly calmer in order to execute intricate human activities" (Gardner, 2011). Mithen has theorized about this cognitive cross-correlation of information in an evolutionary context, proposing that at some point in hominin evolution, the cognitive processing of information between (intrinsic) domains became possible, and he has referred to this as "cognitive fluidity" (1996) (see p.109), though he fails to sufficiently outline the aspect of motivation (i.e. a causal path of evolution). The proposed model addresses the issue of motivation through rewards and outlines a specific cognitive/communicative mechanism that would have promoted the flow and organization of information across intrinsic domains. Because humour was predicated on the general tenet of incongruity, it could have involved many (if not all) of the intrinsic and extrinsic domains of early hominins, assuming the conditional factors of positive emotional valence and moderate arousal were met. Humour was not domain-specific in relation to cognitive operation or extrinsic circumstances and as a result it would have facilitated the flow and organization of information across domains. For example, humour would not have been an essential part of the extrinsic domain of hunting, but assuming positive emotional valence and moderate arousal; it could function within that behavioural domain. The same is true of modern humans; humour is not an essential part of the domain of mathematics, but assuming positive emotional valence and moderate arousal (actually, in modern hominins moderate arousal is not required though it could facilitate), it can function within that domain or any other. As such, humorous behaviour in hominin populations would have cross-correlated information within multiple cognitive domains and enhanced the faculty of integrative, meta-cognitive thought. This would have manifested itself in a pedagogical fashion, yielding perspective and increased comprehension in relation to the information being processed.

The issue of motivations or drives for behaviour just mentioned in reference to Cognitive Fluidity Theory is of interest when considering (extrinsic) domains because typically, specific rewards or

drives are confined to specific domains such as procuring food or a mate: domain-specific drives create domain-specific behaviours. Humour's drive was domain-general, but humorous behaviour would also have stimulated the broader (non-humorous) exploration of cross-domain thought and behaviour due to the rewards yielded by novelty, because novelty is inherently incongrous. Aside from the issue of motivation/drive and the specific mechanics involved, the general evolutionary picture provided by Mithen (1996) is endorsed within this thesis. Intrinsic Domain integration was of great importance in hominin evolution in that it represented an innovation in brain functioning, but used already existing neural systems and structures. This scenario at least partially answers Ramachandran's question: "(t)he hominid brain reached almost its present size — and perhaps even its present intellectual capacity about 250,000 years ago. Yet many of the attributes we regard as uniquely human appeared only much later. Why?" (2000 p.1).

The attributes that Ramachandran refers to include things such as music, shelters, hafted tools[80], dance, tailored clothing, and speech, which all appear to have emerged in hominins in a narrow span of evolutionary time between 30,000 and 120,000 years ago (estimates vary, for a review see O Bar Yosef, 2002) sometimes referred to his as the "cultural big bang" or "cultural great leap forward" or "Upper Paleolithic Revolution". While there will be no further speculation in regards to a time frame for the emergence of humour at this point, it will be shown that this rapid evolution of social structures, technologies, behaviours and the cognitive evolution behind them, was stimulated in part, by general humorous behaviour.

Analogical thought

One key example of a cognitive innovation that occurred in our hominin ancestors is the capacity for analogical thought[81], the origin of which must necessarily have been rooted in biology. In Darwinian terms, an individual of any species has to survive in order to reproduce, so

[80] Wide-spread hafting began roughly 150 kya and the role of duality involved may be deemed to be relevant in the cognitive processes involved in humour.

[81] French says of analogical thought "(i)t encompasses our ability to explain new concepts in terms of already-familiar ones, to emphasize particular aspects of situations, to generalize, to characterize, to explain or describe new phenomena, to serve as a basis for how to act in unfamiliar surroundings, and to understand many types of humor" (2002, p.200).

being able to detect anomalies and avoid them is a fundamental aspect of biology. As such, living entities are perceptually/cognitively focused on reacting negatively to novel stimuli because they represent potential danger. Humour broke from this biologically dictated norm because it constituted a behaviour wherein novel stimuli produced positive reactions, in fact it actually stimulated rewards and benefits. Humour would, however, as it evolved, have increasingly involved the cognitive processing of sameness as well as difference because the cognitive process of voluntarily examining information in order to detect, isolate and communicate incongruities in mental representations would have, by simple inversion, involved detecting levels of sameness[82]. This would have been dynamically similar to the perception of foreground and background that is often commented on in Gestalt psychology. (e.g. Chang et al., 2002; Reinhart, 1984) and the incongruities would have served as semantic retrieval cues (as per Gick & Holyoak, 1983)[83]. It is essential to determine aspects involving levels of sameness, because the more sameness they exhibit, the less appropriate they are for humorous expressions. This may have played an important role in the emergence of analogical thought because in order to identify breaks in patterns, hominins had to indirectly identify the patterns themselves. As such, the processing of incongruity (i.e. difference) involved the metacognitive cross-correlation of information with attention on perceptible differences, and analogy would have gradually emerged as a result of the residual identification of sameness that was necessarily produced. In addition to this, humour predicated on humorous recall would also have involved correlating the attribution of sameness, so humour can be seen to have substantially involved the process of identifying and correlating attributions of sameness and difference. Because humour operated across domains, there would have been correlation and isolation of specific aspects of similarity between multiple sources of information derived from different intrinsic and extrinsic domains. In short, it is proposed that the cognitive/perceptual dynamics underlying the capacity for analogous thought emerged in part as a by-product of the continued reward-driven process of identifying incongruities and sameness stimulated by

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[82] This also brings to mind Gentner's Relational Shift Hypothesis: Gentner (1988) proposed a relational shift whereby children interpret analogy and metaphor first in terms of object similarity and then in terms of relational similarity

[83] Gick and Holyoak state "(t)he essence of analogical thinking is the transfer of knowledge from one situation to another by a process of mapping-finding a set of one-to-one correspondences (often incomplete) between aspects of one body of information and aspects of another". It is interesting to note that a cognitive perceptual error, mistaking one thing for something else similar, could produce accidental humour, that would be stored in memory as both memory and and analogy (1983, p.2).

humour. It is possible that this began with the process of identification, abstraction and categorization and as this progressed hierarchically, the faculty of simple abductive reasoning (i.e. associations of and between categories) began to emerge, which facilitated causal reasoning, which facilitated voluntary analogical thought involving abstracted conceptions.

It can be seen that analogical thought was not merely a spandrel[84] however, because the totality of the resulting conception, incorporating cross-correlated aspects of sameness and differences, formed a singular unified mental whole and this provided the raw material for analogical thought, which can be seen as the organized, integrative processing of such holistic mental constructions. It would perhaps be clearer, however, to say that analogy functioned as a constructive element within the cognitive dynamics of humour, it was not a by-product redundant to the process. In the cognitive phase(s) immediately preceding the emergence of the capacity for applied analogical thought, such mental constructions would have been loosely organized (ie: literally "con-fused"), possessing some level of humorous content, but lacking broader coherence because they were insufficiently organized/integrated. It is proposed that analogical thought would have gradually emerged as a result of continued multi-domain cross-correlative cognition, and eventually involved holistic conceptions incorporating a spectrum of sameness and difference (i.e. abstract conceptions) that would have created abstracted cognitive "realities" or essences that could be accessed in relation to interoceptive information (thoughts) or exteroceptive (perceptions). As such there would have been two levels of meta-cognition involved: 1) the multiple domain cross-correlation of information producing mental constructions involving a spectrum of sameness and difference and 2) the cross-correlation of such constructions resulting in holistic mental constructions that were integrated and cross-correlated in turn, producing abstracted cognitive realities or essences. This scenario can be related to Deacon's assertion that "(c)ompeting sets of overlapping associative relationships on the indexical level translate into mutually supportive higher-order semantic categories on the symbolic level" (1997, p.96).

As was mentioned, humour could have also involved incongruities based on recognition of aspects of sameness: it is possible for incongruity to be manifested in sameness. This can

[84] A spandrel can be generally defined as a phenotypic characteristic in an organism that initially emerges as a by-product of another characteristic.

occur, for example, in the act of imitation: an impersonator can make people laugh in the absence of a funny script or any physical humour because the act of imitation is funny in and of itself. This involves incongruity because the imitative expressions are coming from a novel source, but the humour is predicated on the recognition of the quality of sameness in those expressions. Similarly, an object that looks like a human face (i.e. a pareidolian object) can be seen as funny because of the incongruity in seeing a human face in an object, but it is the recognition of the visual pattern resembling a face that allows the humour to occur. This works at a higher and more abstracted level in linguistic humour where homonyms, malapropisms, double entendres and other devices can be used to evoke humour by creating and exploiting ambiguity[85]. It is also notable that ambiguity is a noted quality that appears in humour and it can be seen as the mingling of sameness and difference. In human thought, mental constructions consist of different qualities of attribution and it is the ability to abstract and cognitively process those attributions that is critical to analogical thought. An apple, for example, has specific object qualities. It is typically red/green, roundish, has a stem, tastes sweet, has a core, and is about 7-8 centimeters wide when full grown. Perception of incongruity in relation to any of these qualities in combination within a situation involving positive emotional valence and moderate arousal has the potential to be produce humour. To try and create comedy about an apple is largely a process involving consideration of the apples attributes, both inherent and contextual. The abstract representation of an apple the size of a thumbnail or the size of house could be considered to be amusing. Within the proposed model, accidental humour predicated on perception of incongruities occurring in relation to specific qualities, would necessarily have involved the cognitive isolation of those qualities. The voluntary creation of humour would have involved the conscious isolation and manipulation of objective qualities (or the perception of them) and it is proposed that this process gradually yielded abstracted mental conceptions incorporating extrinsic phenomena and intrinsic information (i.e. memories) that I have referred to as cognitive “realities” or essences. In sum, accidental humour served to break mutliplicitous information down into its constituent elements (i.e. the objective qualities) subject to any existing perceptual and cognitive constraints, and voluntary humour involved the manipulation of these elements in a communicative format, which gradually created a shared body of abstracted

[85] It is notable that there is a joke type (“what’s the difference between” jokes) that is predicated on the relationshipship between sameness and difference. For example: “What's the difference between a zippo and a hippo? One is heavy while the other is a little lighter” or “What’s the difference between a joke and a rhetorical question?”.

conceptions. In short, humour took holistic perceptions, broke them down into their elements, abstracted those elements and could then reconstruct them into holistic abstract conceptions. This cognitive cross-correlation and manipulation of constituent elements within abstracted conceptions (i.e. qualities), would have then made analogical thought possible[86]. This thesis will refer to analogical thought rather than the more specific notions of analogical mapping and analogical reasoning as further consideration of the dynamics of mapping and reasoning are beyond the primary focus of this thesis.

This aspect of the proposed model once again, puts emphasis on the role of rewards in the evolutionary process and these rewards differed from rewards that stimulated behaviour that was beneficial in relation to food or mating in that the behaviour itself was the reward. Possible strategic/conative aspects aside, humorous behaviour was rewarding in and of itself i.e. it was autotelic[87]. If the emergence and/or enhancement of the hominin capacity for analogical thought and the construction of abstracted mental conceptions did occur in this manner, this process may have also facilitated the development of causal models of thought as is suggested by the interrelations between analogical thinking and causality proposed by several scholars (eg: Keane 1997; Goswami & Brown 1990). The basic underlying connection between analogical thought and causal reasoning is that the understanding of an analogy can only occur if there is understanding of the relations upon which the analogy is based (Goswami & Brown 1990). Further support for this supposition is provided by the connection between neoteny and causal reasoning (Buchsbaum et al., 2012) that that was mentioned earlier (see p.61). While it is tempting to pursue this line of inquiry further it is also beyond the primary focus of this thesis.

In behavioural terms, the humour-driven enhancement of the capacity for analogical thought and causal reasoning in hominins would have resulted in telic, strategic modes of behaviour, perhaps beginning with conative forms of humour that were discussed earlier (see pp. 23-25). The viability of this proposed role of humour in the emergence of the capacity for analogical thought is supported by remarks made by Dan Sperber in personal correspondence (2017) when he opined that the emergence of analogical thought was the result of "a uniquely massive investment in cognition with the systematic gathering of information beyond not just immediate

[86] This is reminiscent of the relation between conceptual blending and analogical mapping discussed by Fauconnier and Turner (2003).
[87] The autotelic aspect of humour will be given further consideration in later sections.

practical usefulness but also without any definite future usefulness". Within the proposed model, humour would have provided exactly this type of system. More broadly, the proposed relationship between humour and the emergence of general analogical thought in hominin populations is important in the general evolutionary picture. It is a novel concept within the existing literature and further speculation and research in this area is certainly merited. Having discussed the cognitive aspects of the ramifications of general humorous behaviour, it is now possible to move on to the consideration of broader social and behavioural aspects.

8.2 Broader ramifications

In moving on to the consideration of the broader ramifications of general humorous behaviour on hominin populations after its initial process of emergence, it is necessary to take a more sociologically and anthropologically based approach than has been employed in preceding sections. By considering possible specific ramifications of humorous behaviour in relation to sociological and anthropological observations it is possible to get a more detailed picture that is not limited to ideas relating primarily to cognitive/perceptual aspects. This is reflective of the nature of humour studies, which encompasses the natural sciences and the social sciences in order to gain a holistic view of a complex phenomenon (Martin, 2010).

Because humour was not domain-specific (it could occur in any social circumstance involving positive emotional valence and moderate arousal), rewards and benefits would have been yielded in a wide range of circumstances and in concurrence with a wide range of activities. In practical terms, this meant that there would have been possible enhancement in the performance of individuals and/or groups engaged in humorous behaviour within that situation or activity. Simply put, the benefits of humour could be bootstrapped to a greater or lesser extent onto any related activity. For example, a group that engaged in humour while hunting had the potential to have experienced enhanced social cohesion, increased pain tolerance, modulated stress levels, improved social memory, and enhanced perceptual sensitivity to the actions of others, which in turn increased their success in subsequent joint-action tasks. It is reasonable to believe that a hunting group with these advantages would be more likely to be successful than a group without them. As such, humour had the potential to function as a positive constituent element within different activities rather than simply being an activity in and of itself. Even though humour typically would have functioned in an autotelic (or "paratelic" as

per Apter, 1989) manner, it could still take place within telic (i.e. goal driven) activities, thus potentially creating the "reversal" dynamic that Apter proposes (1989)[88]. So it can be seen that humorous behaviour had the potential to change the dynamics of a broad range of hominin social experiences, and extend the rewards and benefits that might be yielded into many different scenarios/activities.

Obviously, within this thesis it is only possible to examine a tiny portion of the broad scope of hominin behaviours and social dynamics that might have been affected. These social/behavioural aspects will be examined from an etic perspective and general conclusions will be drawn. Consideration of behaviours and their possible effects on social structures and dynamics will in some cases also lead to consideration of the potential cognitive significance of the whole. The areas that will be focused on are pro-sociality, the definition of self and other, consciousness, neophilia, sexual selection, and parent/child interactions. Proceeding in this manner will necessarily involve overlap and omissions, but will provide a clear analytical framework for this broad subject.

8.3 Pro-sociality

It has already been asserted that hominin humour would have enhanced co-operation, encouraged pro-sociality, and involved a type of automatic altruism (see p.90), and at a more general level the social nature of humour and its associated laughter and smiling responses is well illustrated by Hertzler's description of laughter as "a social phenomenon. It is social in its origin, in its processual occurrence, in its functions, and in its effects" (1970 p.28) [89]. Research has shown that people laugh thirty times as often when they are in social situations as opposed to when they are alone (Provine and Fischer, 1989), and a study of laughing and smiling during structured and unstructured play in 3-5 year olds showed that 95% of laughter and smiling took

[88] Reversal theory proposes that typical psychological/behavioural dynamics involve regular reversals between four apparently opposing psychological states (telic/paratelic, conforming/rebellious, mastery/sympathy, self/other), which constitutes the functioning of metamotivational domains (Apter, 1989).

[89] McGhee outlines four general functions of humor in social interaction. Briefly, they are: facilitation of social interaction; popularity and friendship; socially acceptable expression of aggression and; moderation of assertive/dominating styles of interaction.

place in social interactions (Bainum, Lounsbury and Pollio, 1984). Perhaps the clearest distillation of the social nature of humour can be seen in Chapman's research showing that the "mere presence" of another person facilitates laughter in children (1973). A counterpoint to this pro-social position that is sometimes cited (eg: Chapman, 1983; Foot & Chapman, 1976) is Berlyne's assertion that because laughter can occur in solitary individuals "it seems doubtful that its prime significance is a social one" (1972 p.51). From an evolutionary perspective, Berlyne's position is difficult to sustain, due to the fact that laughter functions in a primarily social/communicative manner in apes (Ross et al., 2010; Provine, 2001) and in human infants (Fogel et al., 1992), which suggests that the ability to laugh in isolation was necessarily a later evolutionary development. Turning to the broader notion of humour, it can be seen that its origins in infancy occur in social environments (McGhee, 1979; Reddy, 2001) and with a few exceptions (eg: Hurley, Dennett & Adams, 2011), humour, in evolutionary terms, is generally viewed as having emerged as a social activity (Martin, 2010). It has even been proposed that all humour is socially predicated (Apte, 1985), involving the recall of social memories, the consideration of possible future social events, and the reflective observation of the self in performance (as per Goffman, 1969). In sum, humour can be seen to result from a cognitive process mediated by affective state, and it is most effectively facilitated in a social milieu.

To put this in an evolutionary perspective, the operation of humour created a dynamic wherein rewards and benefits were yielded by pro-social behaviour, thus fostering the evolutionary development of such behaviour. Hampes sums this up by stating, "To say that humour was favoured by natural selection is to say that it served as an evolutionarily pro-social mechanism" (2006 p.181). Hominin individuals/groups that used humour were pro-social, and they profited from rewards and benefits. Conversely, those individuals/groups who didn't use humour, were less social and did not profit from the same rewards or benefits. Van Vugt et al. illustrate the dynamic that humour would have created when they describe laughter as:

> an effective way to smoothen social interaction between individuals (especially in potentially conflicting relations between strangers), thus enabling them to create and operate in highly cooperative units necessary for survival. In this view laughter might have evolved as an adaptive mechanism to build up social reserves that groups could rely upon in times of crises, a view that is consistent with positive psychology (2014 pp.30-31)

Humour would have created a reward based pro-social drive resulting in social groups being created or expanded, and/or enhanced through increased cohesion, and it would have provided a voluntary system of emotional modulation. As such, within the proposed model, paratelic voluntary communication (i.e. not dependent on factors related to survival, food or mating) functioned as an evolutionary force in creating/expanding/enhancing social structures in pre-linguistic societies. In behavioural terms, the general use of humour would have marked an evolutionary shift towards greater extraversion: the positive correlation between extraversion and humour has been documented by numerous researchers (eg: Craik et al., 1996, Ruch & Deckers, 1993 Saroglou & Scariot, 2002). It is also reasonable to believe that general humorous behaviour may have stimulated an increase in the size of social groups. Dunbar's vocal grooming theory, which was mentioned earlier, covers the relationship between laughter and group size quite specifically:

> The average size of naturally occurring laughter groups is about three (Dezecache & Dunbar, 2012) and, since all three people laugh, all get the endorphin 'hit'. In social grooming, by contrast, it seems that only the recipient gets the 'hit'. Since grooming thus has an effective group size of one, laughter is three times more efficient than grooming in its capacity to bond individuals (2017 p.210).

Within the proposed model, this effect would have been further emphasized by the rewards and benefits that have been outlined that were beyond the stimulation of endorphins. Larger groups would have altered the social dynamics and some of the new aspects associated with increased group size may have been enhanced by humorous behaviour. For example, the increased group sizes resulting from humorous behaviour may have increased selective pressures for physical mobility because larger group sizes required greater mobility due to inter-group scramble competition: larger groups deplete food sources more quickly and have to move on to new ones (Isbell & Young, 1996). At the same time, the increased levels of social cohesion provided by humorous behaviour would have facilitated the co-ordination of this type of activity. From a broader perspective, it is also possible to see humour as having played a positive role in

a process of hominin self-domestication as per Hare's theory expressed in his paper "Survival of the Friendliest: Homo sapiens Evolved via Selection for Prosociality" (2017)[90].

General humorous behaviour would have, by default, increased the number of experiences involving positively modified stress levels (i.e. eustress) and a positive emotional valance. As a result, individuals/groups who created, sought out, or fostered such situations had the potential to gain rewards and adaptive benefits thus fostering the evolutionary development of this behaviour. Put very simply, hominins would have become happier, or at least would have been happier more frequently, and because humour was situationally domain-general, there could have been a positive emotional modulation of a wide range of telic activities as has already been mentioned. Even non-affilliative forms of humour may have had a positive effect by serving as a relatively benign and cathartic outlet for aggression that may otherwise have manifested itself in violent actions similar to the cathartic function of humour described by Singer (1968). Considered as a whole, general humorous behaviour can be seen to have brought about a more positive emotional climate for hominins in a manner similar to that described by Rime: "Emotional events that affect collectively a group or a community constitute a major source of influence for emotional climates" (2007 p.308).

Somewhat ironically, the shift towards a more positively valenced emotional climate involving greater eustress may have also promoted instances of isolated behaviour as per Csikszentmihalyi's notion of "flow" (1996). He proposed that situations of greater eustress facilitate engagement of the state of flow, wherein an individual becomes unaware of their role as a social actor and becomes completely involved in the activity they are engaged in, enabling them to achieve peak performance involving a merging of action and awareness. This meant that the social mechanism of humour would have fostered an emotional climate that had the potential to enhance the capabilities and phenomenological experiences of the less social individuals. While Csikszentmihalyi considers the activity itself as the stimulator of the

[90] Hare proposes that cooperative/communicative skills evolved when natural selection favored increased in-group prosociality over aggression in late human evolution and that a by-product of this selection, is that humans show traits of the domestication such as are seen in other domestic animals.

experience of eustress, increased eustress within the general emotional climate would also have facilitated this type of dynamic. As such, the change in social climate caused by humorous behaviour may have been beneficial for individuals in the autistic spectrum and encouraged/accepted individualistic behaviour as part of humorous behaviour or separate from it.

It is significant that the social/behavioural dynamics just described involved another positive feedback loop: humour stimulated pro-social behaviour in an enhanced emotional climate, which fostered situations where humour could occur, resulting in humour stimulated pro-social behaviour in an enhanced emotional climate, which fostered situations where humour could occur etc. This was not only circular; it was recursive (see pp.97-98) and thus, hierarchical. It would have involved a hierarchical progression where an increasing body of shared social experiences served as the glue within social groups of increasing size and complexity. It is proposed that this type of positive feedback loop is an example of Crespi's assertion that "positive feedback can be instrumental in driving many of the most important and spectacular processes in evolutionary ecology" (2004 p.1). The positive feedback loop described is similar to others described in the academic literature (eg: Crespi, 2004; Crews, 2003; Kaplan and Robson, 2002), and the role of such feedback loops in promoting eusocial behaviour in insects (Bourke, 1999) and rats (Alexander et al., 1991) has been documented.

In sum, it is proposed that humour in hominin societies was a pro-social mechanism that:

i) created, developed, and expanded social groups and provided rewards and benefits to those groups including enhanced internal group dynamics and improved efficiency in coordinated tasks thus fostering the evolutionary development of related behaviours and
ii) caused a positive shift in the emotional climate, which fostered further humorous behaviour, creating a positive feedback loop (the increased levels of eustress caused by the shift in emotional climate encouraged "flow", thus enhancing the capabilities and phenomenological experience of the individual and promoting individualism).

Having discussed the subject of pro-sociality in general terms it is now possible to examine the relationship between cognition and pro-sociality.

Cognition in relation to pro-sociality

The phase of hominin evolution under consideration occurred when bio-cultural evolutionary processes were being added to the purely biological ones, which was a transition from the properties of people, to the relations between people, and as such, the social and the cognitive became inextricably linked.

To recap some of what has been covered relating to the role of humour in cognitive evolution; it has been proposed that the use of humour served to:

- improve memory acquisition, retention, and recall;
- develop the shared humour schema and related development of other shared schemata through cross-correlation;
- involve and facilitate the evolutionary development of analogical thought and causal reasoning;
- engage metacognitive processing involving infinite recursive merge;
- develop symbolic competence, imitative capacity, joint attention and Theory of Mind;
- enhance perceptual sensitivity to the actions of others, which in turn increased their success in subsequent joint-action tasks.

These aspects of cognition in an evolutionary scenario of increased prosociality would have had many ramifications and comprehensive consideration of them is beyond the scope of this thesis, so brief consideration will be given on to the subjects of positive feedback loops, the Social Brain Hypothesis and memory.

Positive feedback loops

It has been asserted that humour stimulated pro-social behaviour within an enhanced emotional climate, which fostered situations where humour could occur, and when it did, there was stimulation of pro-social behaviour in an enhanced emotional climate, which fostered situations where humour could occur etc. This positive feedback loop involved recursive cognitive processing, and would have involved a hierarchical progression in the development of schemata, and related cognitive and physiological processes and structures. As such, humour functioned as a progressive system of learning, and this pedagogical dynamic is similar to the

"upward spiral" described by Fredrickson and Joiner where positive mood enhances learning, which enhances positive mood etc. (2002). This type of correlation between learning and emotional state is supported by Waddington's assertion

> "for information to be transmitted from one generation to the next by teaching and learning... it is essential that the recipient should be brought into a frame of mind in which he is prepared to receive the information which is transmitted to him" (2017, p.1).

As such, humour not only served to communicate information, it can also be seen to have provided the situational component of a positive emotional climate and increased sociality that would have manifested itself in increased cognitive/behavioural plasticity and enhanced potential for social learning. This plasticity and potential would then have continued to hierarchically evolve due to the feedback loop that has been outlined.

In evolutionary terms there are parallels between the positive feedback loop in the proposed model and the 'autocatalytic' hypothesis of brain evolution proposed by Alexander (1989), who cited the role of social-intellectual play in the functional design of the neocortex and the role of group size in inter-species conflicts. Alexander's model is focused on conflict and competition rather than cooperation but humour and conflict/competition are not necessarily incompatible as can be seen in Superiority Theory. In a situation involving conflicts/competitions between groups, for example, the use of humour in a specific group had the potential to enhance their level of social cohesion. The cognitive benefits stimulated by humour (memory, analogical thought and causal reasoning etc.), would also potentially have had a positive effect on such conflicts/competitions. The autotelic nature of humour might appear to be antithetical to the powerfully telic act of inter-group violence, but humour could have potentially yielded positive effects within the broader functioning of a specific group involved, and this is reflected in the long and rich history of humour in military groups (Brown & Penttinen, 2013; Nazareth, 2008). This counter-intuitive dynamic, where autotelic behaviour has the potential to enhance telic behaviour, is an important feature to recognize in the broader implications of general humorous behaviour. It is also a dynamic similar to that which was described in relation to the emergence of analogical thought.

Another proposed feedback loop that is relevant to humour in an evolutionary context is Crew's (2003) proposed positive feedback loop between cognitive capacity, increased lifespan and

inter-generational transfer of knowledge. This was well summed up by Crespi: "(i)ncreasing age led to more and better transfer of information to descendant kin, which enhanced their survivorship and reproduction; in turn, selection for improved knowledge acquisition and transfer drove the evolution of human cognitive capacity and function." (2004 p.630). Crew's hypothesis involves a cooperative framework and selection for improved knowledge acquisition and transfer, which is directly relevant to the proposed model. Humour had the potential to dovetail with this dynamic because it involved communication as well as benefits that could potentially increase lifespan. In addition to previously cited benefits, general humorous behaviour would also have given the elderly a tool (in both production and appreciation) by which they could enhance their social status and increase their level of social cohesion, possibly resulting in a longer life span (thus allowing them to increase the amount of information they could potentially transfer).

In sum, humour would have stimulated pro-social behaviour in an enhanced emotional climate, which fostered situations where humour could occur, and when it did, there was stimulation of pro-social behaviour in an enhanced emotional climate, which fostered situations where humour could occur etc. This positive feedback loop involved recursive processing, and would have involved a hierarchical progression in the development of schemata, and related cognitive and physiological processes. In addition to this, general humorous behaviour in hominins may have been a constituent component of other proposed positive feedback loops involving the co-evolution of social and cognitive faculties (including telic functions not necessarily related to humour, thus constituting a heterocatalytic system)[91]. Essentially the rewards in humour served to create a suite of positive feedback loops because extrinsic domain-general social behavioural aspects became constituent elements in the overall dynamic. As a result of this, during the course of reading this thesis, it should be noted that any/all of the cited ramifications of humorous behaviour would have been enmeshed within a series of interconnected feedback loops. In evolutionary terms, humour ushered far more than just the humorous episodes themselves.

[91] Heterogeneous catalysis is catalysis in which the catalyst does not take part in the reaction that it increases. As such, some of the effects stimulated by humorous behaviour can be seen as heterocatalytic.

The Social Brain Hypothesis

The Social Brain Hypothesis proposes that primate brains evolved not only as a result of processing factual information about the world, but also to meet the computational demands of complex social organizations (Dunbar, 1998(a); Whiten & Byrne, 1988). More specifically, the increased size of social groups that may have occurred as a result of the pro-sociality of humour is relevant to Dunbar's proposition that

> "there is a quantitative relationship between brain size and social group size (group size is a monotonic function of brain size), presumably because the cognitive demands of sociality place a constraint on the number of individuals that can be maintained in a coherent group" (2009 p.562).

Dunbar also clarifies that this theory is applicable not only the development in relation to neocortical size, but also to organizational aspects.

As such, brain evolution can be connected with humour's neotenous aspect within the proposed model. The extended period of parental care in hominins and resulting relaxed selection have been positively correlated with evolutionary brain development by many scholars (eg: Leigh, 2004; Smith & Tompkins, 1995). This notion is further supported by research showing the human brain expands between infancy and adulthood by a factor of 3.3, compared with 2.5 in chimpanzees (DeSilva & Lesnik, 2006), and by the notion that "human encephalization was made possible by a combination of stabilization of energy inputs and a redirection of energy from locomotion, growth and reproduction" (Navarette et al., 2011 p.91), which would have resulted from the situation of relaxed selection that has been discussed (see pp.62-65). Some models of the Social Brain Hypothesis directly cite neotenous trends as having had a positive role in increasing the levels of hominin social complexity (eg: Brune, 2000; Flinn & Ward, 2005), which "forced the emergence of a highly specialised metacognitive capacity" (Brune, 2000 p.301). This relates to humour not only in relation to the neotenous aspect, but also in relation to the dynamics of metacognition that have already been discussed.

One measure that is typically used in the determination of social complexity within the Social

Brain Hypothesis is the presence of tactical deception, which is sometimes termed "Machiavellian Intelligence" (Barton & Dunbar, 1997; Dunbar, 1998(a))[92]. This type of behaviour is universally observable in humans but rare in apes (Whiten & Byrne, 1988). Deception can be used in humour as a metacognitive strategy to create the perception of an incongruity, and in comedy this can be referred to as misdirection. The use of the term "Machiavellian" suggests that this type of behaviour necessarily involves the promotion of the interests of an individual at the expense of others and as such, superiority based humour or "practical jokes" would certainly qualify. There would, however, have been humorous behaviour that involved tactical deception, but not in a "Machiavellian" sense, because it yielded rewards and benefits to all those involved. Such deception would have been no less cognitively complex, but its motivations differed. One example of this would have been humour involving displacement "the ability to refer to things or events not present" (Miles, 1991 p.15). Removing expressions from their original context would have created incongruity and as such, humour would have provided rewards for expressions involving displacement as well as the element of pretence that they incorporated. In relation to this, the role of pretence/fantasy in humour during early childhood development has been documented (eg: Bergen, 2003,2007; Klein, 2003; Semrud-Clikeman & Glass, 2010), which provides supporting ontologically based evidence that this may have occurred in hominin humorous behaviour. Significantly, humour involving this type of pretence was a form of mutually acknowledged deception that could exist in the form of basic elements such as a single gesture or vocalization. By using the simplest possible format in terms of cognition and expression, humour would have served to facilitate the emergence of this type of behaviour and it would have done so in a domain-general fashion, which meant that deceptive behaviour and pretence were used in an autotelic manner and were not reliant on drives directly related to survival, food, or sex.

Returning to the Social Brain Hypothesis, it is acknowledged that the proposed model is more relevant to the development of the hominin mind, as opposed to the hominin brain, though consideration of brain development is directly relevant. In terms of a specific timeline for the emergence of the modern human brain, the ontological timing of molar eruption has been seen to coincide with the conclusion of cortical development (Godfrey et al., 2001; Holly Smith et al.,

[92] Machiavellian Intelligence can be given the general definition of the cognitive capacity to engage in behaviours that involve social manipulation in order to achieve specific goals.

1994). Research on hominin dental fossils has shown that the ontological timeline for brain development reached modern levels approximately 160 KYA (thousand years ago)(Smith et al., 2007). If the early neotenous stage of humorous behaviour preceded this then humour may have played some role in the evolution of actual neurological structures rather than just the configuration of existing structures. The fact that humour is a universal human trait that appears at an ontologically early stage supports the idea that this is likely to have been the case. As such, the Social Brain Hypothesis is directly relevant to the proposed model in a general sense, but it most likely applies to the early neotenous phases of humour's evolution, rather than to the phase when there was general humorous behaviour in all age groups.

To some degree, the Social Brain Hypothesis can be seen to have a circular quality: did increasingly complex social systems foster big brains or did big brains foster increasingly complex social systems, or both? The proposed model breaks this circle because it shows that at a specific evolutionary point the drive created by rewards in humorous behaviour would have provided a causal mechanism that was based on a dynamic of perception and cognition that was not based upon this circularity. Humorous interactions would have stimulated increasing cognitive abilities within a social milieu with no prerequisite of social complexity. Humour served as an extrinsic trigger to initiate the described circular process, and the continued operation of humour would have promoted and accelerated this hierarchical co-evolutionary process, thus creating another type of positive feedback loop.

The role of social information in cognitive evolution is also central to the Cultural Intelligence Hypothesis, (Herrman et al., 2007), which proposes that humans evolved a species-specific set of social-cognitive skills, and that this is reflected in the fact that the cognitive skills of human infants differ from those of higher apes primarily in terms of socially based metrics. Again, humour fits comfortably into the proposed paradigm as a social-communicative behaviour yielding rewards and benefits and utilizing simple units of communication.

In sum, humour can be seen to fit within social-cognitive evolutionary theories such as the Social Brain Hypothesis and the Cultural Intelligence Hypothesis and as such, evidence supporting those theories also provides support for the proposed model. Seen in the context of such theories, humorous behaviour provided rewards and benefits that served to drive and sustain a hierarchical co-evolution of sociality and cognition. This can be seen as another example of the more general tendency towards positive feedback loops that has already been described.

Memory

“Evolution has programmed our brains to find two things particularly interesting, and therefore memorable: jokes and sex - and especially, it seems, jokes about sex” (Foer, 2011, p.76).

The role of memory in humour has already been touched on (see pp. 88-89), and I will briefly recap this information. It has been shown that clinical data supports the idea that humour improves memory retention and recall, antiphonal laughter improves social memory, and in the proposed model the operation of memory acquisition, retention and recall had the potential to yield rewards and adaptive benefits. Referring back to the feedback loop dynamics that have been discussed, humour was inherently social and any increase in the size of social groups would have increased the amount of antiphonal laughter, enhanced the emotional climate of the group and encouraged further humorous behaviour. As a result of the adaptive benefits of humour, this scenario would have resulted in populations with improved memory and the enhanced perceptual sensitivity to the actions of others, which would have increased their success in subsequent joint-action tasks (Valdesolo et al., 2010) (including humour). As a result, the autotelic process of humour had the potential to enhance memory related to telic behaviours with potential adaptive value. The development of analogical thought that was discussed earlier would also have been significant in terms of the evolution of the faculty of memory because analogical conceptions have intrinsic mnemonic value (Carney & Levin, 2003). In simple terms, the cross-correlation of information across schemata would have provided more detailed and parsed conceptions, which would have enhanced the hominin capacity for memory acquisition, storage and retrieval.

Memory is typically considered to involve a number of interrelated systems, which can be divided up into the procedural, the episodic, and the semantic (Tulving, 1985). Procedural memory is implicit, involving unconscious recall related to specific tasks (eg: riding a bicycle) and it is a more evolutionarily ancient type of memory (Tulving, 1985). Episodic memory is explicit and involves the retention and recall of specific episodes. Semantic memory is explicit and involves the retention and recall of internally represented aspects of the world that are not perceptually present and allows for the construction of mental models (Craik, 1967). So, while procedural memory involves memories of how to ride a bicycle through experience, semantic memory involves abstracted notions of what a bicycle and its constituents components actually are. As such, semantic memory involves generalized facts such as “ice is cold” and can be seen

as the product of the cross-correlation of information between schemata, which is involved in both humour and analogical thought. It is evident that general humorous behaviour would have involved procedural, episodic and semantic memory and as such, humour represented a system that yielded rewards and benefits for processing within all levels of memory. In order to clearly illustrate the dynamics involved I will recap the list of rewards and benefits (see pp. 68-78) in a précised form omitting the relevant citations. This list can be referred to when the notion of "rewards and benefits" is brought up during the course of this thesis. General humorous behaviour in hominins would have had the potential to have involved procedural, episodic and semantic memory and as such, the use of such forms of memory would have been associated with the possible stimulation of:

- an elevated mood caused in part by stimulation of the nucleus accumbens, ventral tegmental area (VTA), and amygdala, triggering the mesolimbic dopaminergic reward system;
- a raised pain threshold;
- enhancement of the reward effect for food and drugs;
- regulation of dopamine and serotonin levels causing a positive effect on emotional state and patterns of emotional states;
- preparation of the body for action through an increase in heart rate and adrenaline levels;
- a reduction in anxiety, tension, depression and stress;
- an increase in self-esteem and a sense of empowerment and control;
- an increased ability to initiate, maintain and enhance interpersonal relationships;
- a reduction in levels of hostility in social groups;
- improved mental functioning;
- activation of neural imitation systems and "mirror neurons";
- improved immune functioning due to an increase in T cells, increased levels of Immunoglobulin A, an increase in the flow of the lymphatic system, and the production and activity of NK cells;
- improved respiratory functioning, reduced possibility of pulmonary bacterial growth, and reduced effects of bronchial asthma and obstructive lung disease;
- modulated levels of serum pro- and anti-inflammatory cytokines (in individuals with rheumatoid arthritis);
- reduction in allergic responses associated with atopic dermatitis;

- increased levels of breast-milk melatonin in nursing mothers, thus leading to reduced allergic responses, improved sleep and reduce colic in breastfeeding infants;
- amelioration of post-prandial glucose excursion in diabetics and mitigation of diabetic nephropathy;
- increased energy expenditure of particular benefit to obese individuals or those with reduced mobility;
- lowered risk of myocardial infarction and reduced risk of recurrence;
- an increase in empathy, intimacy, and interpersonal trust;
- enhanced infant/parent bonding helping to ensure survival into adulthood;
- an increase in sexual desirability;
- an increased level of fertility / rate of pregnancy.

In addition to this, the associated rewards would have provided the drive to repeat humorous actions derived from procedural, episodic and semantic memory, and the act of repetition itself "is one of the most powerful variables affecting memory" (Hintzman, 1976 p.47), so the act of repeating humorous expressions would also have had a positive effect on memory.

The emotional aspect of humour has been discussed (see pp.21-23), and emotions have been shown to facilitate the retention and recall of memories: "the current emotional state may be stored with episodic memories, providing a mechanism for the current emotional state to affect which memories are recalled…and by guiding the cerebral cortex in the representations of the world that are set up" (Rolls, 1990 p.169). The emotions involved in humorous behaviour would necessarily have had a positive valence, and emotions with such positive valence have been shown to enhance memory retention and recall (Fredrickson, 2001; Talarico et al., 2009). As such, the operation of humour would have enhanced the faculties of memory and associated the retention and recall of memories with rewards. This in turn would have enhanced the ability to produce and/or appreciate a greater variety of humorous expressions, thus creating another hierarchical positive feedback loop, which can be added to the suite of those already discussed. It is proposed that this positive feedback loop would have served to accelerate the evolution of the hominin faculty of memory and contributed to the hierarchical development of shared bodies of knowledge. Furthermore, the increase in the size of social groups stimulated by humorous behaviour would have magnified this effect.

The relationship between humour and memory can be seen in the many humorous devices that are used in children's educational materials to capitalize on their mnemonic efficiency eg: rhymes, repetition, oronyms, and alliteration (Catts, 1991; Goldman et al., 2006). The use of humour for mnemonic purposes is also documented in areas of adult education (eg: Caplan & Stern, 2008; Snetsinger & Garbowski, 1993) and as was mentioned earlier, it can also be seen that memory plays an important role in stand-up comedy practice (Molineux, 2016).

In sum, general humorous behaviour would have served to enhance hominin capacity for memory acquisition, retention and recall at a cognitive level (due to the cross-correlation of information between schemata), an emotional level, and a behavioural level. The interrelation between humour and memory would also have manifested itself as a hierarchical positive feedback loop which, in tandem with the increase in group sizes that has already been discussed, would have magnified the level of evolutionary development that took place.

Having now examined the subject of cognition in relation to sociality, it is now possible to move on to consider the role of humour in the development of hominin symbolic competence.

8.4 Symbolic competence

The functioning of memory involves the acquisition, retention and retrieval of information, but it is also important to consider the nature of that information. It has already been stated that humour processing involved the cross-correlation of information across multiple schemata, which served to create abstract mental conceptions. This brings to mind Langer's definition of a symbol "…any device whereby we are enabled to make an abstraction" (1953 p.xi) and the fact that abstraction is involved in the cognitive dynamics of humour suggests that further consideration of this subject is warranted.

The subject of symbolic competence can be considered in terms of both cognition and behaviour. There are many instances where scholars have noted a connection between humorous behaviour and symbolic competence, eg: "it can be inferred that laughter…and humour (via incongruity and ridicule) fruitfully coevolved with symbolic activity" (Viana, 2017, p.2) and "primitive humor experiences require symbolic play, which in turn requires the manipulation of images of objects rather than the manipulation of the objects themselves" (McGhee, 1979, p.95). At a cognitive level, the abstracted conceptions that were created

through the cross-correlation of information between schemata were symbolic in nature by Langer's definition. An abstracted conception of a specific humorous expression could, for example, have involved an association between an expression and a specific location and as such, the location, to whatever degree, signified the expression and vice versa. Hummel and Holyoak (2003) described a similar dynamic in their proposed notion of symbolic connectionism and considered in this way, humour can be seen as having provided a "cognitive architecture that codes relational structures" (this is questionable as perhaps humour provides a cognitive dynamic rather than architecture)(p.221) that was necessarily symbolic in nature.

One factor that would have played an important role in generating "the manipulation of images of objects" described by McGhee (1979) was displacement, which was discussed earlier (see p.132). Humour involving repetition from memory recall had the potential to take place in situations that were different than the original situation, and the likelihood of this may have been increased by the fact that a situational incongruity had the potential to add additional humour. As an example, the repetition of a humorous action that first occurred in a hunting situation might involve referring to objects and/or actions relating to that hunting scenario: throwing a spear could be represented by the action without requiring an actual spear or substituting a stick. This was, in a literal sense, significant: an action served to signify an object, an action, and an event. This process is summed up well by the following statement: "A present object that is only vaguely comparable to an absent one can evoke a mental image of it and be assimilated to it, resulting in the creation of a symbol" (Leslie, 1987 p.412). Here, the clear relationship between pretense and symbolic expression is shown and pretense can be considered a form of meta-representation as per Leslie (1987). The linguist Derek Bickerton further clarifies the inter-relationship between symbols and displacement when he states "the most salient characteristic of symbols is that they can refer to things outside of the here and now. This capacity is something linguists generally refer to as "displacement" (2009 p.50).

So displacement can be seen as instrumental in symbolic communication, and at the same time it was (and is) a humorous device in and of itself: the displacement of an object or action into a novel context had the potential to stimulate the perception of incongruity. As such, displacement, and thus, symbolic expression, was a necessary by-product of any humorous episode that involved the use of objects and or actions that were recalled and repeated from previous humorous episodic memories if they were displaced from the initial context of the action and/or object. As a result, general humorous behaviour would have served to create

growing bodies of iconic and indexical actions and/or objects within humour schemata. These icons and indices would, however, have also had intrinsic cognitive dynamics in humour processing because they could be considered congruous or incongruous in relation to one another: a facial expression involving narrow squinting eyes would be incongruous with one involving very wide-open eyes. Humorous expressions could be created through the manipulation of such mixtures of incongruity and salience (both expressions emphasize the eyes) within iconic and indexical actions (or objects)[93]. Again, this may have occurred accidentally at first and gradually become ritualized and recognized, which brings to mind an observation Mary Douglas had in relation to humour: "(c)ontinual experimentation with form has given us now an intuitive sympathy for symbolic behaviour which is, after all, a play upon form" (2002 p.147).

Moving from Langer's broad definition of a symbol to Peirce's more involved taxonomy of signs makes it possible to consider specific categories which can be placed in a hierarchical context. Peirce distinguishes the icon ("a mere community in some quality" (1991, p.30)), the index ("whose relation to their objects consists in a correspondence in fact" (1991, p.30)) and the symbol ("whose relation to their objects is an imputed character" (1991, p.30)). Within the proposed model, it can be seen that early humour (both accidentally and volitional) involved a communicative system that utilized the manipulation of relationships between icons and indices. Consideration of this type of evolutionary development of symbolic competence is seen in Terrence Deacon's book "The Symbolic Species" (1997) where he outlines how interactions between icons and indices leads to the use of symbols. This is summed up in the following way: "symbolic relationships are composed of indexical relationships between sets of indices and indexical relationships are composed of iconic relationships between sets of icons" (Deacon, 1997 p.75). It is proposed that humour provided an autocatalytic system that effected the hierarchical development of thought and communication in relation to symbolic elements (icons, indices and symbols) and as per Deacon's model, this would have facilitated the hominin capacity for symbolic competence. Essentially humour would have provided the cognitive, behavioural/motivational framework that made such a path of hierarchical development

[93] These dynamics should be considered in a co-evolutionary context with those outlined in relation to analogical thought. The constituent elements within analogical thought were necessarily symbolic in nature and any enhancement in the faculty of analogical thought/expression was also an enhancement in the faculty of symbolic thought/expression.

possible. Deacon partially presages this possibility when he comments “I suspect that implicit in the notion of humour there is a symbolic element, a requirement for recognizing contradiction or paradox” (1997 p.73).

In social/behavioural terms, the use of symbolic communication through humorous interactions had ramifications beyond the operation of humour. As has already been stressed, humour was a domain-general behaviour and could occur in any situation/activity where there were perceived incongruities or recollection of previous humorous experiences in concurrence with positive emotional valence and moderate arousal. This meant that the autotelic process of humour would have had ramifications within potentially telic activities including the use of a progressing hierarchy of symbolic expressions. As was discussed earlier, humorous associations were more likely to be retained in memory, which meant that symbolic expressions were more likely to be retained in memory, and thus could be recalled later and potentially be applied in a functional (telic) manner. In this way, the operation of humour would have served to introduce and enhance symbolic communication in numerous domains of hominin behaviour. Once again, the autotelic element is important because it created an evolutionary scenario wherein competences and behaviours and their constituent elements could emerge regardless of their immediate level of adaptive value; once these competences and behaviours emerged and profliferated, adaptive values then had the potential to emerge. This, of course, was not a substitute for an evolutionary dynamic based on adaptive values, but it existed in addition to it (and in co-operation with it) and added the potential for greater cognitive and behavioural plasticity.

In sum, the pro-social dynamic within the proposed model would have caused the creation of larger, more cooperative groups of hominins whose use of humour involved the cognitive manipulation and communication of elements within common mental schemata, which necessarily created abstract mental conceptions of a symbolic nature. This process would have involved the use of icons and indices in humorous thoughts and actions, as well as the use of displacement, which was both inherently comic and inherently symbolic. General humorous behaviour in hominins would have created a situation wherein symbolic communication was associated with rewards and adaptive benefits and it is proposed that the resulting dynamic enhanced and accelerated the hierarchical development of hominin symbolic competence. At this point it is also worth remembering the relationship between humour and Theory of Mind, and humour and the capacity for analogical thought, both of which have already been

discussed. Individuals capable of this combination (Theory of Mind, symbolic competence, the capacity for analogical thought, and humorous behaviour) can arguably be seen as having made the transition from hominin to modern human.

In concluding consideration on this topic, it is noted that the proposed model can be related to Deacon's statement:

> …despite their cognitive limitations, our ancestors found a way to create and reproduce a simple system of symbols, and once available, these symbolic tools quickly became indispensable. This insinuated a novel mode of information transmission into the evolutionary process for the first time in the billions of years since living processes became encoded in DNA sequences (1997 p.45).

As such, the cognitive capacity to manipulate symbols can be seen to be inherently social. It is also possible that the capacity for symbolic thought may have led to the abstraction of aspects of sociality such as individual and group identity.

8.5 Identities and interactions

The increasing amount of symbolic communication brought into hominin life as just outlined would, necessarily, have involved greater complexity in the expression and interpretation of identities of individuals and groups. The broader subject of identities and interactions will be considered in terms of the role played by humour in the creation and development of self-identity, social identity and group identity in pre-linguistic hominin society. This will involve consideration of the role of humour in interactions that took place between individuals as well as within and between groups (i.e. inter-group and intra-group interactions) as it is these interactions that provided much of the necessary perceptual/cognitive input required for the creation and development of these identities.

Self-identity

Self-identity can be defined as the totality of an individual's independent and interdependent self-construal involving the particulated, abstracted aspects by which an individual defines themselves. It is probably accurate to say that the notion of self-identity is dependant on Theory

of Mind. For example, an individual can be defined to a certain extent by their biologically dictated features (e.g. I am tall, I have brown hair), but it can also involve aspects of individual behaviour (e.g. I can climb trees well) and social interaction (e.g. I am attractive). A comprehensive overview of the development of distinct self-identity (including subjective agency and self-representation) is beyond the scope of this thesis but it is asserted that the creation of self-identity is a socially mediated process (Damon & Hart, 1982; Lewis, 2012). In discussing the ontogenic formation of the subjective self Fonagy et al. (2007) noted that positive emotion promotes the emergence of mentalization and specifically cite humour as a factor as a relational influence on the development of such mentalization[94], and Woods describes humour as "an instrument to protect and develop the self" (1983 p.111). Fonagy et al. (2007) also point out that a system of symbolic representation is necessary for such a process to occur; without this, qualities can exist but they cannot have attributions. The important roles smiling, laughter, and humour play in early childhood development as outlined by McGhee (1979) and Reddy (2001) also imply that humour has a direct effect on the development of self-identity. The formation of a self-identity is necessarily predicated on the differentiation of self from others and is thus central to the notion of Theory of Mind, and its importance in hominin evolution is well illustrated by Gardner's comment: "The capacity to know oneself and to know others is as an inalienable a part of the human condition as is the capacity to know objects or sounds, and it deserves to be investigated no less than these other 'less charged' forms." (2011 p.243). In simple terms, humour would have provided a powerful tool for hominins to express individual characteristics relating to their cognitive and emotional states and provided a paratelic framework wherein such expressions could be manifested. As such, these characteristics were made explicit and shared between social conspecifics, but humorous expressions would also have provided valuable information related to social classification that could be applicable to the formation of self-identity as per Ashforth and Mael's assertion that "social classification enables the individual to locate or define him- or herself in the social environment" (1989 p.21)[95].

General humorous behaviour would have caused an increase in the number of emotionally positive social interactions, and these interactions would have involved the cognitive processing

[94] The term mentalizing is used as a substitute for Theory of Mind.

[95] There is feedback loop where self-identity contributes to social identity, which serves to contribute to self-identity.

of the mental and emotional states of others (i.e. Theory of Mind) as well as the voluntary manipulation of these states. In addition, humour would have stimulated prosociality and involved face-to-face contact and joint attention. All the preceding would have been important in the social mediation of the creation of self: specific characteristics signifying identity could be created and communicated. The identification and interpretation of such characteristics would have been facilitated by the incorporation of symbolic elements as was just discussed (see pp.137-141)[96]. The dynamics involved in this process would have been similar to the ones described in the development of analogical thought: in considering "what is not", one must necessarily consider "what is". This process may, in fact, have been a behavioural component that facilitated the development (or co-evolution) of the capacity for analogical thought in hominins.

The mechanics behind this process can be seen in the basic dynamics of humour. From a cognitive perspective, humour was predicated on the ability to distinguish incongruous perceptual input (eg: big/small, thin/fat, self/other) and as a result of this, beginning in early infancy, humour would have functioned as a system that stimulated the ability to recognize and share such incongruities, including incongruities of qualities relating to self and other, and this process would have been associated with rewards and benefits that have been discussed. The cognitive processing of these qualities stimulated by humour would have involved the creation of abstracted mental conceptions relating to the associated individuals (self or others). It would ultimately result in a holistic abstracted mental conception of specific individuals (self or others) involving symbolic elements that could be cross-correlated in relation to abstracted conceptions associated with other individuals and groups. It is also rational to assert that such conceptions are necessarily symbolic in nature. Sticking your stomach out to pretend to be fat is a good example; the extended stomach symbolizes fatness. As such, hominins would have developed a cohesive conception of self-identity beyond the mere perception of uncorrelated phenomenological aspects. For example, the act of displaced imitation of an individual (i.e. without the presence of the individual who was being imitated), would necessarily have involved

[96] It could be argued that in evolutionary terms, self-identity is the symbolization of the individual (see Burke & Reitzes, 1981).

the formation and recall of a shared abstracted conception of that individual.[97] Humorous expressions were also affective in nature, and the importance of emotional cues in extracting information relevant to the formation of self is illustrated by Bretherton and Beeghly's statement on how the self/other correspondence first emerges: "(i)f emotional display in another's face, voice, or behavior tends to generate a similar state in the beholder …then the child might eventually come to attribute the felt emotion to the other" (1982 p.915). It is also possible that the activation of mirror neurons, which has been shown to occur during humorous interactions through smiling (Leslie, Johnson-Frey & Grafton, 2004), would have contributed to this dynamic in a direct neurological manner.

Imitation and identities

The role of imitation in humour has already been discussed (see pp. 87-88) but it is worth further consideration in light of its role in the creation, recognition, and expression of identities. Imitation has been shown to play a role in the creation and continued development of self-identity (Charman et al., 2000; Meltzoff, 1993, 2002). Voluntary imitation can be seen as a behavioural and communicative extension of the scenario presented by Bretherton and Beeghly (1982): imitation involves attribution and the sharing of associated information among social conspecifics. What was earlier described as "pre-imitative" behaviour occurs spontaneously in many animals (Dijksterhuis, Bargh, & Miedema, 2000; Moore, 1992; Range et al. 2011), but true imitation has been claimed to be unique to humans (Blackmore, 2001; Tomasello & Call, 1997). In contrast to the folk wisdom of "monkey see, monkey do", even pre-imitative behaviour is rare in apes and is typically limited to actions related only to food or sex (Tomasello, 1994; Heyes, 1993), while humans have the capacity for imitation at birth (Meltzoff & Moore, 1977) and children "can be observed repeatedly to copy what others do for no other apparent reason than 'that is what is done'" (Whiten et al., 2003 p.98). Like humour, imitation can exist as an autotelic activity. Pre-imitative behaviour in primates is qualitatively inferior to imitation seen in humans as is illustrated by Foster's description of it as "limited to fairly gross gestural imitation of other

[97] Decety and Sommerville (2003) explain how similar and distinct brain regions are involved in the differentiation between self and other, both when imitating and when being imitated.

primates" (1994 p.187) and by research showing that adult chimpanzees lack the imitative precision of human children (Horner and Whiten, 2005; Nagell, Olguin & Tomasello, 1993). Within the proposed model it can be seen that general humorous behaviour would have stimulated and facilitated the hominin capacity for imitation. Driven by rewards and benefits, humorous behaviour would have stimulated the ideomotor framework of hominin actions within a common representational format for action and perception and this in turn would have stimulated the evolutionary development of the hominin capacity for imitation. From a biological/neurological perspective, this would have involved the use/development of mirror neurons (Iacoboni, 2009; Ramachandran, 2000) and possibly Von Economo cells (also referred to as spindle neurons) (Iriki, 2006), which are evolutionarily recent (Allman et al., 2010) and have been shown to be involved in the processing of humour (Watson et al., 2006) [98]. Furthermore, the development of Von Economo neurons is primarily post-natal, occurring within the first 8 months after birth (Allman et al., 2010) and would thus have been potentially subject to modulation by extrinsic factors such as humorous behaviour.

Imitation is central in the operation of humour (eg: Everts, 2003; Alford & Alford, 1981). Aristotle defined comedy as “an imitation of inferior people” (from Heath, 1989 p.344) and Sidney called comedy “an imitation of the common errors of our life” (from Harrison, 1998 p.59). Imitation is, however, not only inherent in comedy it is also explicit; imitation is a common tool in comedy (impressionists and impersonators), and can involve the imitation of self (Glenn, 1988). A further correlation between humour and imitation can be drawn from clinical research showing that autism has a negative correlation with both humour production/appreciation and the imitative faculty (Rogers et al., 2003; Williams et al. 2001). It is worth reiterating that in the evolutionary context under consideration humour was domain-general and would have introduced imitative behaviour into a wide sphere of activities which stands in contrast with the pre-imitative behaviour of apes, which is typically limited to actions relating to food or sex. So it can be seen that imitation is at the heart of comic expression and the development of the capacity for imitation through humour would have had ramifications beyond humour itself (this is representative of a heterocatalytic system). Humour would have provided a mechanism that enabled hominins to distinguish the specific attributes of self and other(s) in a domain-general,

[98] It is possible that stimulation of the imitative faculty played a role in the development of mirror neurons by way of Hebbian learning (see Borenstein & Ruppin, 2005).

shared communicative format and thus served to facilitate in the formation, continued creation, and expression of self-identity.

Summary

The creation of self-identity is a socially mediated process and humorous behaviour would have allowed hominins to create expressions based on abstracted individual characteristics relating to their cognitive and emotional states, thus providing specific symbolic information that could be applicable to the formation of self-identity. Cognitively, the enhanced capacity to detect incongruities would have facilitated the ability to distinguish and cognitively abstract the specific characteristics of self and others. Humorous behaviour, through displacement or otherwise, would have involved the creation of abstract mental conceptions of constituent elements of identity and eventually of cohesive, holistic abstract (i.e. symbolic) conceptions of specific identities relating to self or others. The capacity for analogical thought that humour engendered would have co-evolved with the capacity for the creation and identification of symbolically based identities. General humorous behaviour would also have introduced domain-general imitation into hominin life which would have aided significantly in the process of creating self-identity.

Social Identity

Social identity can be defined as the identity of the individual as determined by relationships with social groups and activities (e.g. I am a football fan). The notion of social identity represents something of a middle ground between the identities of the individual and those of the group. Social Identity Theory proposes that individuals create a social identity based on relations to social groups (Tajfel & Turner, 1979): a collective, depersonalized identity based on group membership. An individual's social identity is interrelated with their self-identity, which, for the most part, retains primacy in this relationship (Gaertner et al., 1999), though it is possible for this collective de-personalized identity to result in behaviour that could result in death or injury (i.e. self-harming behaviour), such as engaging in war (Alexander et al., 2004).

In the evolutionary context in question, humour would have communicated information about cognitive and emotional states within specific contexts, which had the potential to create associations between groups and elements of the information being communicated. For

example, humour that involved actions and/or objects related to specific objects, activities or individuals already associated with a social group had the potential to signal affiliation, neutrality, or hostility toward that group. As such, humour would have served as a way for hominin individuals to engage in communicative behaviour that could affect their social position/identity. As with self-identity, the creation of cohesive, abstract social identities would have been facilitated by the process of cross-correlation of mental schemata and capacity for analogical thought engendered by humour. In the case of social identity, this process would have had broader social ramifications as is reflected in Ashforth and Mael's description of the functions of social identity: "it cognitively segments and orders the social environment, providing the individual with a systematic means of defining others" (1989 pp.20-21). From this perspective it can be seen that humour would have operated as a communication system that enabled individuals, in tandem with their social conspecifics, to cognitively segment and organize abstracted mental representations based on information related to social classification. The domain-general nature of humour in combination with displacement would have allowed the transmission of information related to social classification between multiple groups and thus the ability to transcend the externalities that previously defined social groups (shared activities, age, physical abilities, family etc.). More importantly, volitional humorous behaviour would have offered the opportunity for the individual to be an active agent in defining their social position and transcend the dynamics wherein social status was based more on biological factors.

Anthropological studies on the role of humour in human social relations have typically focused on the "joking relationship" (eg: Brant, 1948, Gundelach, 2000; Radcliffe Brown, 1940). While it is possible to consider joking relationships to be predicated by expression through language (eg: Fine & Soucey, 2005), Apte defines the joking relationship as "a playful patterned behaviour that occurs between two individuals who recognize special kinship or other types of social bonds between them" (1985 pp30-1)[99]. Using this definition, the joking relationship is not predicated on the use of language and can be considered to apply to pre-linguistic hominins. As

[99] Radcliffe Brown (1940) defines the joking relationship as: a relation between two persons in which one is by custom permitted, and in some instances required, to tease or make fun of the other, who in turn is required to take no offence (p.195).

such, general humorous behaviour would have constituted a means of acknowledging kinship and social bonds in a communicative format. The notion is supported by Freedman's description of humorous behaviour as "a means for interacting persons to alter, create and structure social relations" (1977 p.155) as well as by Radcliffe-Brown's assertion that joking relationships between married couples and between clans/tribes are "modes of organizing a definite and stable system of social behaviour" (1940 p.200).

Humour would, however, not only have been a factor in the structuring of human relations, it would also have served to communicate information about the existing structure of those relations. Apte refers to the joking relationship as one of the "major manifestations of kinship" (1985 p.29) and as such, the study of joking relationships has been used to learn about kinship roles because they represesent a manifestation of them (eg: Davidheiser, 2003; Galvan, 2006). So it can be seen that general humorous behaviour in hominins would have affected social structures, which then in turn served to provide information that could be conveyed in subsequent humorous expression, which then affected social structures etc. From this, two interconnected positive feedback loops can be identified. The first was just described, but there would also have been a loop where the development of individual identities contributed to the development of social and group identities, which then contributed to the development of individual identities and so on, and the rewards and benefits associated with humour served to turn this circle into a positive feedback loop. It is proposed that this pair of positive feedback loops would have accelerated the evolutionary development of faculties relating to the creation of self, social and group identities. As such, the proposed model offers a specific, if partial, explanation for the occurrence of what Malone et al. refer to as the "shift from limited plasticity in a generalized social ape to expanded behavioral plasticity as an adaptive niche" (2012 p.1251).

Summary

General humorous behaviour provided a system by which hominin individuals could signal affiliation, neutrality, or hostility toward a specific group (or groups) and as such, it was a means by which individuals could voluntarily affect their social position and create/display their social identity. In this way, humorous individuals were active agents in defining their social position and transcended social status based more strictly on biological factors. The creation of cohesive, social identities from abstracted elements would have been facilitated by the process of cross-correlation of mental schemata and the capacity for analogical thought engendered by

humour. Humour would have also provided a means of acknowledging kinship and social bonds in a communicative format, and the domain-general nature of humour meant that transmission of information could transcend typical group divisions.

Furthermore general humorous behaviour would have helped to structure human relations, and also served to reflect such structures and related dynamics. This circularity would have manifested itself in two interconnected positive feedback loops relating to the development of self, social, and group identities. It is proposed that this pair of positive feedback loops in combination with the other previously mentioned factors would have accelerated the evolution of hominin faculties relating to the creation of self, social and group identities.

Group Identity

While it is possible to use the terms Social Identity and Group Identity interchangeably (e.g. Ashforth and Mael, 1989), in this thesis Social Identity refers to identity within social interaction between individuals and Group Identity refers to identity related to intra-group or inter-group interactions. The creation and development of hominin social groups would have resulted from kinship, shared activities (Chapais, 2013) such as hunting or cooking (which was a practice common at the evolutionary time period in question (Wrangham et al., 1999)), and as a result of common factors such as age, gender, or dwelling proximity. As was already mentioned, humorous behaviour would have made it possible to transcend such dynamics; individuals could form groups simply out of choice…because they liked one another. In relation to this it is noted that Apte (1985) differentiates the nature of joking relationships within kinship and social groups and says that while kinship based joking relationships are largely obligatory and based on existing kinship based conventions, social group joking relationships are more voluntary and have greater fluidity. As such joking relationships can be seen as primarily having reflected existing social structures within kinship situations, but in social groups, joking relationships would have served to create social structures as well as reflecting them.

In the definition and expression of hominin social structures, humour had the potential to function in both an esoteric ("what one group thinks of itself and what is supposes others think of it" (Jansen, 1959 p.206)) and an exoteric capacity ("what one group thinks of another group and what it thinks that other group thinks it thinks" (Jansen, 1959 p.206)). In the course of shaping and displaying social structures humour would have manifested a paradoxical element

that has been discussed by several scholars (eg: Fry, 1987; Lynch, 2002; Meyer, 2000). The essence of this paradox is well summed up by Lorenz, "laughter forms a bond and simultaneously draws a line" (1963, p.253), and within the framework of social structures in the evolutionary scenario under consideration this can be considered to have been manifested in the twin paradoxes of identification/differentiation, and control/resistance proposed by Meyer (2000)[100]. Meyer proposed that the communicative functions of humour should be seen on a continuum from identification and unification to differentiation and social exile and pointed out that divisive humour actually has the potential to unite one group against another. It could also be argued that such dynamics do not necessarily represent a paradox; language can convey joy or sadness, it can unite or divide. It represents a medium, not a mode.

The role of humour in defining, differentiating, affiliating, and dividing groups is extremely broad and well documented (see below), and in Martineau's opinion "humour is part of every social system, and can be analyzed as one social process affecting the system" (1972 p.103). Research has shown that humour influences social group structure and dynamics in social groups based on: gender (Collinson, 1988; Walker, 1991), nationality (Gundelach, 2000; Malefijt, 1968), occupation (Schnurr, 2009), sexuality (Archakis & Tsakona, 2005; Kehily & Nayak, 1997), sports teams (Williams, 2009), video-game communities (Kirkpatrick, 2012), and political affiliations (Davies, 2007; Hart, 2007) to name just a few. As was discussed earlier, the stage of general humorous behaviour (as contrasted with humour in its emergent stages) would have been concurrent with (and related to), the advent of larger social groups (see pp.122-123). Anthropologically based research showing that joking relationships are significantly less common within the nuclear family (Murdock, 1965), and particularly uncommon in between related females in preliterate and traditional societies (Apte, 1985) suggests that the increase in the size of social groups would have facilitated further humorous behaviour. Humour also would have had the potential to enhance the efficiency of a group (Avolio et al. 1999; Romero & Pesconsolido, 2008), suggesting that it also had the potential to aid in the survival of the group as well as its individual members.

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[100] It is worth remembering Meyer's statement: "Humor is viewed as a cognitive experience involving an internal redefining of sociocultural reality and resulting in a "mirthful" state of mind" (p.311).

It is logical to believe that following Stage 8, humorous hominin expressions would have involved simple comic devices rather than more complex ones, and as per the widely accepted notion of cognitive/behavioural phylogenic/ontogenic parallels (see pp.48) it can be seen that these may have been substantially similar to those used in humour in early childhood in humans eg: repetition, exaggeration, imitation and general incongruity (for an overview see Mcghee, 1979). As a result of this, there would likely have been a great deal of commonality between examples of humour in different groups. Humorous expressions would have been recognised as such even if the significance of the content was less clear. Some content may have been easily understandable because even though different groups necessarily had different bodies of shared knowledge, they would also have shared common experiences related to fundamental aspects of life such as the objects and behaviours related to food, sex, age, physical self, and the environment. In my own professional experience performing comedy in variant social environments, comedy frequently functions as a method of seeking and acknowledging shared knowledge and experiences, and this view is supported by Mintz (1985). The cross-cultural appreciation of humour can also be clearly seen in the success of comedy videos of animals on YouTube, and silent film comedy (North, 2009), which do not rely on language, and emphasize universal non-linguistic incongruities. In some ways, the pre-linguistic evolutionary scenario was more conducive to the successful sharing of humour than the modern scenario because humour was simplified by a less developed capacity for vocalizations and symbolic expression, and a relatively scant number of culturally specific information/artefacts which were typically related to commonly held aspects of survival and reproduction.

That said, there would have also been limitations in the universality of humorous expression due to the differences in shared common knowledge that did exist. The content and dynamics of the humorous interactions of a specific group would have reflected the shared body of information that was common to that group: humour was only completely accessible to those who held the requisite knowledge in common. This dynamic is well illustrated by the line that often follows humour that fails to get a positive response: "you had to be there" as well as by Malinowski's notion that "anthropology is the science of the sense of humour"[101] (1937, p vii). Humour puts

[101] It is acknowledged that Malinowski makes this comment in a loose analogical sense, but the comment remains relevant regardless of this.

cultural differences in high relief and it would have created dividing lines between groups as per Bergson et al's assertion: "However spontaneous it seems, laughter always implies a kind of secret freemasonry, or even complicity, with other laughers, real or imaginary" (1911 p.4). The use of the phrase "secret freemasonry" connects this idea with those of Flamson and Barrett, who developed an "encryption" theory of humour (2008), which proposed that humour serves to "signal encrypted knowledge and to communicate useful information in the context of recognizing and acknowledging social alliances" (Flamson et al., 2011 p.249). While Flamson and Barrett's ideas relate primarily to verbal signaling of information, the aspect "recognizing and acknowledging social alliance" is still applicable in the evolutionary context under consideration. Flamson and Barrett stress that the aspect of encryption in humour ensures honesty in communication; knowledge of relevant aspects cannot be faked.

Regardless of the notion of encryption, due to the role of incongruity, hominin humour would have been a medium by which it would have been possible for hominins to express acknowledgement of the recognition of qualities of individuals and/or groups as being different or unusual. As such, it would have served to define and communicate the notion that those individuals and/or groups were "other", and to assert/confirm specific affinitive and/or differential aspects. In practical terms, the general humorous techniques employed would likely have been similar to those described by Apte in his anthropological study of humour: "imitation and exaggeration…to suggest the physical appearance, clothing[102], behaviour, body movements and gestures…considered to be characteristic of the target groups" (1985 p.119), and dependent on the content, inter-group humour had the potential to act either as a social "lubricant" or as an "abrasive" (Martineau, 1972 p.103). It was asserted earlier that hominin humour would have been essentially pro-social, but this does not mean that it would have always been completely affilliative in its intentions or interpretations. In developing a psychological model of humorous behaviour Martin et al. identified four styles of humour: affilliative, aggressive, self-enhancing, and self-defeating (2003). These categories can be seen to represent functional and motivational aspects of humorous expressions. The first three categories have evident relevance to humour in the time frame under consideration, but self-

[102] The use of clothing began sometime between 83 and 170KYA (source: Toups, M.A., Kitchen, A., Light, J.E. and Reed, D.L., 2010. Origin of clothing lice indicates early clothing use by anatomically modern humans in Africa. *Molecular biology and evolution*, *28*(1), pp.29-32).

defeating humour ("use of humor to enhance relationships at the expense of self" (Martin et al., 2003 p.48)) is a more complex, telic form requiring a conscious understanding and complex strategic manipulation of ideas within social dynamics, which makes it less likely to have been as common during the evolutionary stage in question.

The likelihood of "abrasive" elements is suggested by the presence of elevated levels of arousal and the ambiguity with aggression as per Gruner (1978). This notion is further supported by the presence of aggression in childhood humour (McGhee, 1979) and the previously cited examples of captive chimpanzees expressing amusement after urinating on, or throwing feces at, humans (Butovskaya & Kosintsev, 1996; Miles, 1986). Humour used as a form of pseudo-aggression would have served to help define social groups, with milder forms determining or enforcing in-groups and more aggressive forms determining or enforcing out-groups. In relation to this idea, Malefijt has proposed that humour can function as a screening procedure in allowing admittance to a group (1968).

In terms of intentionality, humour derived from the perception of differences in other individuals and social groups cannot be proved to have always necessarily constituted intentional aggressive mocking, there is also the possibility that it it may have been the result of the simple perception of differences. Mocking requires a specific intentional stance that may or may not have been present. The intentional use of humour for the purposes of teasing or mockery as it is seen in a modern context is arguably, a more complex, telic form that may have become common at a later point. As a counterpoint to this notion, however, Polimeni and Reiss (2006) have proposed that teasing behaviour in apes might have been a precursor to humour. Freud described this type of humour as "tendentious"[103] and proposed that by "making our enemy small, inferior, despicable or comic, we achieve in a roundabout way the enjoyment of overcoming him" (1916, p.147). Regardless of where intentional mocking/ridiculing between social groups lies in the hierarchy of emergence, it is a behaviour that eventually became a widespread human activity (Davies, 1990, Dundes, 1975), which can be seen as a way of expressing and/or diffusing aggression.

[103] Tendentious is defined as expressing ideas that are likely to be disagreed with.

The notion of humour as a method of diffusing aggression is an important one in relation to social groups, and the idea that aggressive forms of humour enable the expression of aggression without conflict/violence has been put forward by Radcliffe-Brown (1940) and others (eg: Freud, 1960, Martin, 2010), and Cann et al. state "self-enhancing humour can be used to diffuse conflict which could benefit both individuals" (2008 p.140). This suggests that it is possible that humour would have diminished conflict between individuals and groups, and thus it would have had a positive effect on the ability of those involved to survive and reproduce. Certainly, the positive emotional valence that predicates the functioning of humorous interactions emphasizes the potential to diminish aggression, and this would have applied to both intra-group and inter-group dynamics. It is worth speculating that the diffusion of aggression caused by humour may have had a beneficial effect on "outsiders" within or close to a given group such as individuals with psychological/physical impairments or other visually apparent phylogenic anomalies because any existing aggressive intent could be manifested in humorous expression rather than aggressive actions (as per Stebbins, 1996). As such, the identity of such outsiders would be socially redefined because they would become associated with humour, and as a result to the rewards and benefits that humorous behaviour could stimulate. Teasing and/or laughing at people with disabilities might sound cruel in a modern context, but for our hominin ancestors humour would have had the potential to create a social role for disabled individuals; a function that exempted them from violence that might otherwise have occurred. People with disabilities were potentially outsiders in relation to many social groups and thus subject to the type of humorous attack described by Bourdieu:

> the art of making fun without raising anger, by means of ritual mockery or insults which are neutralized by their very excess and which, presupposing a great familiarity, both in the knowledge they use and the freedom with which they use it, are in fact tokens of attention of affection, ways of building up while seeming to run down, of accepting while seeming to condemn (1984, p.183).

Similarly, the introduction of general humorous behaviour would have given the elderly a tool (in both production and appreciation) by which they could enhance their social status, possibly resulting in a longer life span, which would have allowed greater transfer of knowledge (see p.127). Once again, there would have been elements of adaptive benefit yielded by humorous behaviour. If the basic premise that humour served as a substitute for aggression and enhanced social cohesion and cooperation is correct to any substantial degree, humorous behaviour in hominin populations would have resulted in greater social cohesion and a reduction in

intraspecific and interspecific competition. This would have represented a situation of relaxed selection, which would have resulted in an increased level of genetic plasticity in hominin populations (Badyaev, 2009; Hunt et al., 2011).

Summary

As per Lorenz's observations on laughter (1963), general humorous behaviour in hominin populations would have served to both form bonds within groups and draw lines between them. Commonality in humorous mechanisms and content would have allowed for some degree of universality in humour perception, but humour would also have reflected the shared bodies of information within specific groups and as such some humorous expressions would have been only completely accessible to those who held the requisite knowledge in common. Humour would have put cultural differences in high relief but also have provided enhanced social cohesion within this situation involving increased symbolic complexity in thought and expression. General humorous behaviour would have had an impact in both an esoteric and an exoteric capacity and would have enabled individuals/groups to voluntarily manipulate and communicate information relating to group dynamics. This would have increased the fluidity of such dynamics and facilitated the transcending of boundaries between existing groups. While predominantly pro-social, hominin humour would have functioned as both social "lubricant" and social "abrasive" and served to help define social groups, determining or enforcing in-groups and/or enforcing out-groups and functioned as a screening procedure in allowing admittance to a group. Mocking/ridiculing humour would have served to diffuse aggression thus diminishing conflict between individuals and groups increasing the likelihood that humorous individuals/groups would survive/reproduce. The diffusion of aggression caused by humour may have had a beneficial effect on social group dynamics relating to the elderly and individuals with psychological/physical impairments or other visually apparent phylogenic anomalies, again increasing the likelihood that such individuals would survive/reproduce. In a more general sense, humorous interactions within and between groups would have been adaptively beneficial and engendered a situation of relaxed selection, leading to an increased level of genetic/phenotypic plasticity in hominin populations.

Summary of identities and interactions

In sum, it is proposed that the general use of humour in hominin societies would have played an important role in the evolution of the ability and propensity to develop self-identity, social

identity, and both esoteric and exoteric group identities. The dynamics involved in related processes would have reflected the existing level of complexity of the cognitive, psychological, behavioural, and social dynamics, and the twin paradoxes of identification/differentiation, and unification/social exile as proposed by Meyer (2000) would have been applicable in the evolutionary scenario under consideration. The forms of humour expressed would have involved imitation and exaggeration, and would likely have been less telic than modern forms. Humorous interactions would have had the potential to function as either a social lubricant or abrasive but in balance, it was more likely to have been predominantly affilliative, with abrasive forms serving as a way of diffusing aggression rather than merely expressing it. This view is in agreement with the statement "(l)aughter serves to enhance a sense of social identity which facilitates cooperation among strangers" (Van Vugt et al., 2014 p.29). This scenario would have been adaptively beneficial to individuals associated with groups engaging in humorous behaviour as well as for the elderly and individuals with psychological/physical impairments or other visually apparent anomalies. This resulting dynamic of relaxed selection would have led to an increased level of genetic plasticity in hominin populations. Perhaps most significantly, general humorous expression provided a medium by which individuals and groups could voluntarily affect social statuses and dynamics and thus transcend the previously existing dynamics that were dictated primarily by biological factors. In addition, it is worth noting that the preceding is once again indicative of the transition that hominins made in becoming modern humans, and shows that the dynamics of humour were at the centre of why this transition was came about.

8.6 Consciousness

The subject of consciousness was touched on earlier (see pp.109-110) but it is appropriate to return to it very briefly at this point in light of notion of the voluntary creation of identities that was just discussed, because the capacity to create and express an abstracted conception of self is indicative of consciousness. In agreement with a hierarchical approach to the evolution of consciousness (eg: Feinberg & Mallatt, 2016; Wilbur, 1997) (i.e. an approach that suggests a gradualist, particulated, hierarchical evolution of consciousness rather than the saltational emergence of a holistic system), the general emergence of humorous behaviour in hominins contributed to the construction and development of identity as well as its symbolic expression and manipulation in social interaction. This allowed the conscious "I" to become a definable, expressible and shared quantity (for a review of this type of dynamic see Cohen, 2002). The potential role of humour in the emergence of hominin consciousness is implied by Barlow's

statement “the innate desirability of consciousness, together with the impossibility of attaining it except by communication, is an important factor in causing man to be social and gregarious” (1980 p.93). While this statement suggests a connection between humour and consciousness, within the proposed model it is appropriate to re-work this notion into a novel configuration: humour caused hominins to be social, gregarious and communicative, which made it possible to attain an innately desirable level of consciousness.

The proposed model assumes human consciousness to operate as the product of an evolutionarily hierarchical system[104] and the relevant cognitive factors that emerged due to humour at the late evolutionary stage under consideration were:

1) the creation and development of a humour schema that operated in an autotelic manner across extrinsic domains i.e. it was not solely determined by factors relating to survival and/or reproduction;
2) the cross-correlation and communication of mental representations (inclusive of symbolic elements) derived from multiple schemata;
3) the development of Theory of Mind.

Within the proposed model, humour would have played an important role in the emergence, development and proliferation of these three factors. General humorous behaviour would have stimulated cognitive/communicative development that meant that, in contrast with apes, when a hominin peeled a banana, they would have been specifically aware of the “I” that was peeling the banana. They could also cross-correlate the abstract notion of “peeling” with other abstract notions, and even consider “peeling” as a metaphor. Furthermore, because the proposed model shows humour to have emerged as a cognitive extension of a process that was initially one of physical cause and effect i.e. tickling, a continuous line can be drawn in hominin cognitive evolution from phenomenal experience to consciousness; from the biological to the bio-social. This could be considered to represent a resolution, or at least a compromise between the phenomenal and illusionist views of consciousness: that consciousness must be **either** a property of events or processes **or** an attribution that is made. When considered from an

[104] This list is necessarily grossly simplified in order to fit within the scope of this thesis and does not consider aspects such as imitation, joint attention and theory of mind, which were discussed earlier.

illusionist perspective as defined by Frankish (2016)[105], the outlined emergence and proliferation of humour could be seen as a process by which there was a withdrawal from the purely phenomenal, but this transition was itself, rooted in the phenomenal.

While the preceding section represents only a brief overview on the topic, it does propose another crucial element into the transition hominins made to become modern humans. The picture of exactly how this transition took place, in behavioural, cognitive and social terms, becomes clearer with each aspect that is introduced (consciousness, pro-sociality, Theory of Mind, analogical thought etc.) and gradually constitutes a holistic model. The section on neophilia that follows adds yet another contributing aspect to this.

8.7 Neophilia

General humorous behaviour in hominins was a conscious activity, and in social and behavioural terms, it had the potential to increase attention on novelty framed within a positive emotional valance. Objects, events and ideas that are novel, or have a novel element (or elements) necessarily have a degree of incongruity to them. Novelty is often cited as an element of humour (eg: Caron, 2002 ; Hoika & Akhtar, 2012; McGhee, 1971; Morreall, 1989) and is perhaps best thought of as "related variable" of incongruity (Forabosco, 2008 p.56)[106].

General humorous behaviour in hominin societies would have caused a shift towards behaviour involving novel experiences and interpretations: hominins would have become more neophilic. The quality of neophilia is more strongly evident in humans than in any other species (Miller, 1998, 2000; Zuckerman, 1984). Research has shown that the mesolimbic dopamine system is involved in mediating novelty-seeking behavior in other animals (eg: Bardo et al., 1996; Fink & Smith, 1979; Hooks & Kalivas, 1995), but this research has focused on a correlation between

[105] In defining Illusionism Frankish writes "According to illusionists, our sense that it is like something to undergo conscious experiences is due to the fact that we systematically misrepresent them (or, on some versions, their objects) as having phenomenal properties. Thus, the task for a theory of consciousness is to explain our illusory representations of phenomenality, not phenomenality itself."(2016 p.11).

[106] Morreall considers incongruity to be based on previous experiences rather than a lack of them (Morreall, 1989) , so by his definition an adult experiences more incongruity, while a child experiences more novelty but this distinction is a semantic one in the context under consideration because incongruity, with or without the element of previous experience, had the potential to function in the same capacity in the production and/or appreciation of humour.

reduced dopamine levels and reduced novelty-seeking behaviour rather than the release of dopamine as the result of the cognitive processing of novelty. As such, in other animals, novelty doesn't yield rewards but is simply more frequently sought during states involving raised levels of dopamine: novelty isn't the catalyst, it is the result. In cognitive/behavioural terms, Deacon has proposed that "a propensity to search out new 'perspectives' might be a significant advantage for discovering symbolic relationships" (1997, p.94), which would have provided another way by which humorous behaviour facilitated the enhancement of hominin symbolic competence (see pp.137-141). In psychological terms, "openness", is related to neophilia and has been proposed to be one of the Big Five personality traits in humans (Buss, 1991; Schmidt & Buss, 2000)[107]. Furthermore, it has been proposed that these five traits can be distilled into two higher-order factors (DeYoung, 2006; Digman, 1997), with one of these two factors termed "plasticity"[108], which "captures the novelty-seeking and unconventional qualities of openness and the impulsive and energetic qualities of extraversion" (Silvia et al., 2008 p.77). It is notable that extraversion is positively correlated with humorous behaviour (Soroglou & Scariot, 2002; Vernon et al., 2008) and that neophilia is inherent in the operation of humour, as both are considered to be of central importance in the definition of human personality. This, of course, is relevant to the previously discussed subject of the creation of identities.

The significance of neophilic behaviour in humans is reflected in Miller's excellent description of the scope of modern human neophilia:

> human neophilia is the foundation of the art, music, television, film, publishing, drug, travel, pornography, fashion, and research industries, which account for a substantial proportion of the global economy. Before such entertainment industries amused us, we had to amuse each other on the African savannah — and our neophilia may have

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[107] The Big Five Personality traits have been discussed by numerous researchers (eg. Goldberg, 1981; McCrae & Costa, 1987; Schmidt & Buss, 2000). Schmidt and Buss list them as: (CANOE) Conscientiousness, Agreeableness, Emotional Stability (versus Neuroticism), Openness to Experience, and Extraversion.

[108] DeYoung sums up the proposed higher order factors as follows: Neuroticism (reversed), Agreeableness, and Conscientiousness form one factor: Stability. Extraversion and Openness/Intellect formed a second factor: Plasticity (2006).

> demanded ever-more creative displays from our mates. This hypothesis can explain the mysterious 'cultural' capacities that are universally and uniquely developed in humans, such as language, music, dance, art, humor, intellectual creativity, and innovative sexual play (1998 p.109).

Miller is speaking loosely when he describes an evolutionary scenario where "we had to amuse each other on the African savannah" but it is just such a scenario that is being outlined within this thesis. The language he uses implies an imperative (we had to amuse each other), which is in line with the role of rewards in the proposed model but could be more accurately rephrased as "we were driven to amuse each other".

The shift towards neophilia that humour engendered would have had cognitive implications as well as behavioural ones. The processing of novelty has the potential to enhance memory formation and recall (Nyberg, 2005; Schott et al., 2004; Tulving et al. 1996), and Schott et al. have proposed that memory enhancement may occur because "encoding of novel stimuli exerts an excitatory influence on midbrain dopaminergic neurons" (2004 p.385). This supports aspects of the proposed model relating humour to memory that were presented earlier (see pp.134-137). Furthermore, it has been shown that novelty increases processing speed due to dopaminergic rewards (Bunzeck et al., 2009), and Otmakhova et al. (2013) have proposed that there is a positive feedback loop caused by these rewards which adds to (or blends with) the suite of feedback loops made possible by humour that have already been discussed.

Neophilia is also of interest in evolutionary terms because it has specific biological markers that can be identified in hominin remains: polymorphisms of the dopamine receptor gene DRD4 have been specifically linked to novelty seeking behaviour (Ebstein et al., 1996; Okuyama et al., 2000; Pogue-Geilly et al., 1998). The DRD4 gene in humans is unusual in that it shows a high amount of expressed polymorphism (Seaman et al., 1999) and is markedly different from the DRD4 of chimpanzees (Livak et al., 1995). More specifically, the seven-repeat (7R) allele of DRD4, which it is thought to have derived from a more ancient form (the 4R allele) approximately 40 to 50 KYA, (Wang et al., 2004)[109], has been associated with novelty seeking

[109] Wang et al. proposed that the 7R allele originated as a rare mutational event that increased due to high frequency by positive selection and supported this claim with evidence drawn from cross-cultural DNA testing .

(Laucht, Becker, Blomeyer, & Schmidt, 2007) and greater pro-social orientations (Sasaki et al., 2013). Within the proposed model, humorous behaviour would have facilitated the emergence of such a gene mutation. It is suggested that research on the DRD4 gene in relation to humour and/or hominin evolution could provide valuable evidence in supporting or refuting aspects of the proposed model. While it is not being suggested that the DRD4 should in any way be considered to be a "humour gene", research into this gene may be a blunt instrument in gaining information relating to prehistoric humour: "brain pathways are specified in the genome; detailed connections are fashioned by, and consequently reflect, socially mediated experience in the world" (Eisenberg, 1995, p.1564). Research has already shown a positive correlation between novelty seeking related polymorphisms of the DRD4 and homo sapiens migration distances (Chen et al., 1999; Matthews & Butler, 2011). Matthews and Butler have proposed that the "out of Africa" migration, which took place between 50,000 KYA and 12,000 KYA, selected for individuals who were more positively adapted to novelty (2011). This supports Roll's assertion "(f)inding novel stimuli rewarding is one way that organisms are encouraged to explore the multidimensional space in which their genes are operating" (2000 p.182). In evolutionary terms, it has been proposed that "DRD4 variants linked to altered dopamine signaling capacity could have coevolved with cultural forms of human adaptation" (Kitayama, 2014) and humour can be seen as just such a cultural form. The time frame that has been given to the emergence of the seven-repeat (7R) allele of DRD4 should not necessarily, however, be considered as an indicator for when humour may have emerged, though it may correlate in some way with the broader emergence of general humorous behaviour. Humorous behaviour may have pre-dated the emergence of the 7R allele, but the resulting behavioural changes caused by this emergence would have favoured both humour creation and appreciation. If this scenario did occur, there would have been a direct correlation between the spread of this gene sequence and the proliferation of humour, and the adaptive benefits of humour would have positively modulated the dynamics of such a spread.

In ontogenic terms, the preference for novelty in infancy has been positively correlated with higher intelligence in later life (Fagan, 1984) and this can be seen as indicative of a similar dynamic in infant development during the evolutionary phase in question and/or as reflective of a possible parallel between ontogeny and phylogeny. Similarly, Caron proposed, "Humans may

initially use laughter as a way to manage the arousal created by novel stimuli, so that the pleasure of laughter and play encourages exploring and consequent cognitive development" (2002 p.269). From this perspective, the neophilic element of humorous behaviour can be seen to have performed a pedagogical function during the course of hominin evolution and the presence of reward based feedback loops would have had a ratcheting effect that would have accelerated the evolution of related hominin cognition.

In social terms, it is proposed that a humour-derived, enhanced level of neophilia would have manifested itself in an increase in individual and group acceptance of variations in physical appearance and behaviour. This would have worked in tandem with the enhancement of social interactions with the elderly and people with observable disabilities that was already discussed. Related to this, the imitative aspect of humour may also have played a role in creating and enhancing empathy (as per: Carr et al., 2003; Iacoboni, 2009). As was stated earlier, this type of dynamic would have engendered relaxed selection and further increased the potential for phenotypic plasticity and associated genetic diversity. Humour-derived neophilic behaviour, however, would not only have fostered an environment that encouraged this type of diversity, it also would have yielded adaptive value beyond the humorous. Neophilic behaviour initially stimulated by humour would have gradually evolved to a point where it would have occurred independently from humorous behaviour, and the ability and propensity to process novelty in cognitive and communicative terms would have resulted in greater cognitive and behavioural flexibility and an enhanced ability to adapt to change i.e. it had direct adaptive value. In this way, any related genetic changes would have been more likely to be retained and proliferated in hominin populations. The following passage illustrates this type of dynamic while also providing a reasonable summary of the Baldwin Effect:

> If animals entered a new environment — or their old environment rapidly changed — those that could flexibly respond by learning new behaviors or by ontogenetically adapting would be naturally preserved. This saved remnant would, over several generations, have the opportunity to exhibit spontaneously congenital variations similar to their acquired traits and have these variations naturally selected. It would look as though the acquired traits had sunk into the hereditary substance in a Lamarckian fashion, but the process would really be neo-Darwinian. (Richards, 1989 p.399)

Before leaving the subject of neophilia, the related subject of innovation should also be touched

upon. In general terms, “neophilia” is the love of that which is novel, and “innovation” comes from the Latin root “innovare”: to make new. A positive association has been documented between neophilia and innovation in different species (Day et al., 2003; Lefebvre, 2000), and it has been proposed that innovation drives social learning and, eventually, cumulative culture[110] (Day et al., 2003; Kaufman & Kaufman, 2004; Lefebvre, 2000). Kaufman and Kaufman (2004) have proposed a hierarchical model for this type of progression, which has three steps. The first step is recognition of novelty, which can be observed in many animals and is typically evidenced by neophobia. The second step is observational learning, which they describe as occurring in macaques, whales and pigeons, though they acknowledge the role of human intervention. The third step is innovation, and Kaufman and Kaufman cite several examples relating to survival and food acquisition (2004). This last point is significant because it shows that their model fails to take into account the domain-specific nature of non-human innovation (i.e. non-human innovation is always directly related to survival, food acquisition or mating), which is of central importance in limiting the potential of such a progression to create culture. The essential difference between neophilia and innovation is that neophilia relates to a cognitive/emotional response to stimuli, while innovation relates to an action(s) and/or process(es). Voluntary humorous behaviour bridges that gap because it involves the creation of domain-general novelty as well as the associated cognitive/emotional response.

Summary

Novelty is a concept that overlaps significantly with incongruity and it can perhaps be best thought of as a “related variable” of incongruity (Forabosco, 2008 p.56), so it can be seen that the general use of humour in hominin societies would have necessarily caused a shift towards neophilic behaviour. It is proposed that such behaviour had the potential to enhance intelligence, memory acquisition, retention and recall, and increase individual and group acceptance of variations in physical appearance and behaviour thereby providing adaptive benefits and creating greater phenotypic plasticity and genetic variance in hominin populations. The (7R) allele of DRD4 gene has been connected with neophilia and pro-social behaviour, and

[110] “Cumulative cultural evolution is the term given to a particular kind of social learning, which allows for the accumulation of modifications over time, involving a ratchet-like effect where successful modifications are maintained until they can be improved upon” (Caldwell & Millen, 2008, p.3529).

thus, should have some correlation with humorous behaviour. If this is the case it can be inferred that the general use of humorous behaviour may have emerged at around 50 KYA, and promoted neophilia that manifested itself in the "out of Africa" migration that began at this time. Furthermore, humour at this time manifested innovation as well as neophilia, which was of adaptive significance, so any associated genetic aspects such as polymorphisms of the DRD4 gene would have been likely to have been retained due to the Baldwin effect. Neophilia would have also had an effect on social relations including sexual selection and sexuality, though this is a broad topic worthy of more specific consideration.

8.8 Sexuality and sexual selection

Consideration of any phenotypic variations in an evolutionary context necessarily involves consideration of the effect a variation might have on the individual's chances of reproducing. Sexual selection provides a direct mechanism by which phenotypic variations such as humorous behaviour can be selected for, and thus have their related genetic aspects passed on to succeeding generations. When considering the effect of humorous behaviour in the evolutionary phase under consideration, it is necessary to account not only for the behaviour itself, but also related aspects that were effected by that behaviour or in relation to it (i.e. direct and indirect ramifications). For example, it was shown earlier that humour was fundamentally pro-social, and pro-sociality is positively correlated with higher levels of inter-personal attraction (Graziano et al., 1997; Jensen-Campbell et al., 1995). Furthermore, Graziano et al. (1997), proposed that pro-sociality is compatible with dominant behaviour, which in turn is correlated with increased levels of female attraction to males (Jensen-Campbell et al., 1995; Sadalla et al., 1987). Obviously, each degree of separation represents a weakening in the level of connection with humorous behaviour that can be assumed[111], but the preceding are examples within a pattern of general positive correlation between humour and its associated factors with higher levels of inter-personal attraction, which will be discussed in relation to Miller's (2000) theory of mental fitness indicators.

[111] The multiple effects of humour on sexual selection could also be considered within the notion of a heterocatalytic model: it is yet another example of co-scaffolding dynamics.

It was shown earlier how humour would have helped to define, expand, and evolve social groups. Being in a group ensured affliative social contact with increased security as well as commonly held bodies of information through shared experience, all of which would have facilitated humorous interaction (see pp.146-152). In relation to sexual selection, this meant that humorous individuals were more socially connected, experienced quantitatively higher levels of situations involving positive emotional valence, and were therefore more likely to have mating opportunities. As such, humour not only provided a tool for attraction but also in a broader context, helped create social structures that enhanced the prospect of situations where the tool could be applied[112]. The development of positive relationships is far more likely to occur in an intra-group situation (Hewstone et al. 2002, Mullen et al. 1992) and West-Eberhard describes intraspecific reproductive competition as "the cornerstone of the theory of evolution by natural selection" (1979 p.222).

In constructing his theory of sexual selection, Darwin was attempting to "explain extraordinary sexually dimorphic characters troublesome to his theory of natural selection" (Arnold, 1983 p. 71). Within the proposed model, humour first emerged as a neotenous behaviour and did not play a significant role in sexual selection because humorous expression was minimal after sexual maturity. As such, humour cannot be seen as the "product" of sexual selection, but the general emergence of humorous behaviour (in all ages) would have introduced humour as a factor within the process of sexual selection. Broadly speaking, sexual selection theory proposes that in most species one sex (typically females) invests more time and effort in parenting (and gestation), making them more limited in the number of offspring they can conceive (Miller, 1998). This results in members of this higher-investing sex becoming more selective when choosing a mate; so in the typical scenario males compete for female attention. This dynamic also has the potential to result in self-reinforcement of female preferences leading to pronounced sexual dimorphism (Fisher, 1915), the classic example of this being the peacock's tail. This process is often referred to as "Fisherian Runaway"[113], though an alternate to Fisher's model have been presented (eg: Grafen, 1990; Zahavi, 1975[114]).

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[112] This pun is unintentional, but as the topic is humour, it really should be acknowledged.
[113] Fisherian Runaway refers to the process within which maladaptive traits are sexually selected for, leading to positive feedback from subsequent generations which has the potential to expand exponentially.
[114] Zahavi's handicap principle is the costly signal notion referred to by Miller, which hinges on the importance of the cost of the signal, rather than the signal itself.

The possible role of humour in sexual selection has been the subject of some study and conjecture (eg: Greengross & Miller, 2011; Li et al, 2009; Miller, 2000(a)), and Greengross has summed up the general conclusions well: "a good sense of humor is consistently ranked as one of the most desirable traits in a potential mate, especially for women" (2014 p.181). Conversely, a social environment involving adults, but with a lack of sexual opportunity would typically result in a lack of humorous expression, and this is reflected in the fact that joking relationships are significantly less common within the nuclear family (Apte, 1985; Murdock, 1965). Apte sums this up by saying "The greater the distance between…collateral relatives, the higher the possibility of marriage, and therefore of the joking relationship" (Apte, 1985 p.39). Humour has been seen to be positively associated in attracting potential mates (inter-sexual selection) (Feingold, 1992; Greengross & Miller, 2011; Hewitt, 1958; Li, Bailey, Kenrick, & Linsenmeier, 2002; Sprecher & Regan, 2002) as well as in competing with others of the same sex (intra-sexual selection) (Greengross & Miller, 2008). As such, general humorous behaviour in hominin individuals would have directly increased the possibility of directly attracting a mate. It would also have elevated their social status and in so doing, indirectly improved their chances of being selected as a mate.

Perhaps the best known theory regarding humour and sexual selection is the theory of mental fitness indicators (Miller, 2000(a)), which proposes that a good sense of humour is connected with sexual attraction because it is a hard-to-fake signal of intelligence, creativity and mental health (Greengross & Miller, 2011). This hypothesis is supported by evidence that humour is positively correlated with creativity (McGhee, 1979; Murdock & Gamin, 1993; Ziv, 1976) and cognitive intelligence (Feingold & Mazzella, 1991; Greengross, Martin, & Miller, 2012; Greengross & Miller, 2011; Kaufman et al. 2010; Masten, 1986)[115], and adaptive humor styles (which would be those most often used in courtship) are positively correlated with emotional intelligence (Gignac et al., 2014; Greven et al., 2008). It is, however, important to stress that Miller is referring to the general process of sexual selection rather than the specific behavioural dynamics of mate selection. Within the process of mate selection humour would have been

[115] It should be acknowledged that the correlation between humour and intelligence is not 1:1 – humour can operate within multiple cognitive/behavioural modes but it doesn't necessarily enhance them. Humour might be a path to understanding, but paths can be slower than the sidewalks or superhighways they engender.

primarily selected for due to its direct attributes and associations rather than as result of its efficacy in signaling the qualities outlined by Miller. The rewards yielded by humour that have been discussed in some detail support this proposition. Additionally, in discussing the connection between humour and intelligence Li et al., noted “in the studies where women rated men who used humor to be more desirable for relationships (Bressler & Balshine, 2006; Lundy et al., 1998), women also rated the humorists as less intelligent than nonhumorous men” (2009 p.926), which indicated that humor can be desirable regardless of whether or not it is perceived to indicate intelligence. As such, hominin individuals would not have been using humour as a marker of intelligence, creativity etc. of a prospective mate; they were simply enjoying humorous interactions and those who facilitated them. As such, intelligence, creativity and mental health would have been selected for incidentally, but humour served to allow such indirect selection and the resulting yield of adaptive benefits, to occur. In relation to this subject it is also notable that humorous behaviour occurs in, and in the proposed model was derived from, situations unrelated to sexual selection as shown in its proposed neotenous origins thus, its role as an indicator for intelligence, creativity and mental health again is shown to be incidental. Essentially, humorous interaction could have functioned like a pre-sexual compatibility test.

Bearing this in mind, it can be seen that general humorous behaviour in hominins would have served as a pro-social device that enhanced social status, contributed to the formation and maintenance of groups, and facilitated positive interactions between potential mates. In direct terms, humorous expression would have stimulated rewards (dopaminergic and otherwise), which enhanced the prospects of sexual attraction. Humour was also associated with a moderate level of arousal, which could further facilitate sexual attraction. Furthermore, as was mentioned earlier, there is also research that indicates a correlation between humour compatibility and the stability of long-term partnerships (Murstein & Brust, 1985; Rust & Goldstein, 1989; Ziv, 1988) and the children born from long-term relationships were more likely to survive and reproduce because they had protection and provision from both parents.

As such humour can be seen to have been pro-social behaviour facilitating reproductive opportunities. This would have applied directly to the dynamics of courtship, but limiting it to courtship assumes total autonomy of the individuals involved, and emphasis should also be placed on the role of social structures and conventions in the selection process (Baumeister, 2000; Puts, 2010). Returning to Greengross and Miller, their statement: “intelligence may be sexually attractive mainly insofar as it is manifest through verbal humor” (2011 p.191) indicates

that it is possible they are in agreement with the idea that humour was directly selected for in mate selection, though the value of prelinguistic communication skills in the evolutionary phase in question would suggest that the preceding statement should not limit itself to verbal humour.

Before concluding consideration on the topic of sexuality and sexual selection, it is also worth noting that the (7R) allele of the DRD4 gene which was discussed in relation to neophilia, has also been positively correlated with "greater sexual desire, easier arousability and better sexual function" (Zion et al. 2006 p.782) as well as infidelity and sexual promiscuity (Garcia et al., 2010). Bearing this in mind, the rewards yielded by humorous behaviour in hominins would have created a drive for incongruity manifested as neophilia, and this drive for novelty would have co-occurred with greater sexual desire, easier arousability, better sexual function, infidelity and sexual promiscuity. Novelty-seeking behaviour has also been associated with a greater diversity in sexual practices (Hamer, 2002; Hamer & Copeland, 1994)[116]. Hamer asserts that "genes involved in novelty seeking would influence sexual partner diversity" (2002 p.263), but in the context under consideration, this runs contrary to research that indicates a correlation between humour compatibility and the stability of long-term partnerships (Murstein & Brust, 1985; Rust & Goldstein, 1989; Ziv, 1988), so it is difficult to see a clear picture in this regard. It is also possible that development of Theory of Mind that is proposed to have been stimulated by humour could have increased the importance in cognitive/communicative factors in mate selection and/or increased the likelihood of deception related strategies (Brune & Brune-Cohrs, 2006). It is difficult to come to conclusions in this area due to the number of variables involved in this evolutionary context that cannot be determined. The proposed neophilia related increase in the social status of individuals with observable phenotypic variations (physical and behavioural) along with their ability to engage in humorous expression would have increased their likelihood of mating and, thus, of having their genes reproduced. If this hypothesis is correct, it would have resulted in an increased resistance to disease (Spielman, 2004; Tishkoff & Verrelli, 2003), and

[116] It is worthwhile to give further consideration to the role of neophilia in relation to sexual practices and the effect it may have had on the evolution of human sexuality. For example de Waal notes that in bonobo populations the average copulation lasts 13 seconds making sexual contact in bonobos rather quick by human standards. De Waal, F.B., 1995. Bonobo sex and society. *Scientific American*, *272*(3), pp.82-88.

would also be reflected in an increase in genetic markers for such phenotypic variation in the fossil record.

Summary

It is proposed that sexual selection was an important aspect of the broader dynamics of humour in an evolutionary context because it allowed for the specific selection of humour in individuals, providing a direct mechanism by which any related genetic aspects were passed on to succeeding generations. The prosocial effect of humour within specific interactions between individuals, as well as in defining, expanding, and evolving social groups would have led to higher general levels of reproductivity, as well as specifically higher levels in humorous individuals. Associated neophilia would have broadened the range of phenotypic variants favoured in mate attraction, allowing the related genes to be passed on, which would have resulted in an increased resistance to disease. The positive role of humour in mate selection also meant that any associated aspects such as intelligence, creativity, symbolic competence, communicative ability, pro-sociality etc. were also, directly or indirectly, being selected. In contrast with Miller's theory of mental fitness indicators, it is proposed that humour was primarily directly selected for, and did not merely serve as an indicator for intelligence, creativity, and mental health.

8.9 Parental aspects

Pre-natal

Sexuality and sexual selection do, of course, often lead to the subject of parenting. The role of humour in a parental context begins with the process of mate selection and in this regard it was already noted that research has indicated that there is a correlation between humour compatibility and the stability of long-term partnerships (Murstein & Brust, 1985; Rust & Goldstein, 1989; Ziv, 1988), and that children born from long-term relationships were more likely to survive and reproduce because they had protection and provision from both parents. Also previously noted was research that indicated the potential positive effect of humour on fertility rates (Friedler et al., 2011). In terms of the effects of general humorous behaviour on pregnancy in the evolutionary phase in question, the rewards and benefits associated with humour, laughter and smiling can be divided roughly into i) those relating to social interactions, and ii)

those relating to mental and physical health. This omits consideration of the majority of cognitive benefits such as enhanced memory and an increased level of symbolic competence. It could be argued that these cognitive benefits had the potential to yield positive effects in respect to the survival of the parents and their offspring but such effects are, for the most part, too speculative to be of value in this thesis but could possibly merit further study.

The previously cited aspects relating to physical and mental health include:

i) an elevated mood and raised pain threshold (Dunbar et al., 2011;Weaver & Zillmann, 1994; Weisenberg, Tepper, & Schwartzwald, 1995) caused in part by stimulation of the nucleus accumbens (NAcc), ventral tegmental area (VTA), and amygdala, triggering the mesolimbic dopaminergic reward system (Mobbs et. al, 2003) resulting in endogenous opioid release in the thalamus, caudate nucleus, and anterior insula (Manninen, 2017) and the release of β-endorphins (Miller & Fry, 2009);
ii) a reduction in anxiety (Arnie et al., 1999; Yovetich, et al., 1990), tension (Wooten, 1996), depression (Falkenberg et al, 2011; Deaner & McConatha, 1993), and stress levels due in part to decreased levels of cortisol and epinephrine (Berk et. al, 1989; Nezu et al., 1988);
iii) an increase in self-esteem (Frecknall, 1994; Kuiper, et al., 1992), and a sense of empowerment and control (Sherman, 1998; Wooten, 1996);
iv) improved immune functioning due to an increase in T cells (Berk et. al, 2001), increased levels of Immunoglobulin A (IgA)(Dillon, Minchoff & Baker, 1986, Lefcourt, Davidson-Katz & Kueneman, 1990), an increase in the flow of the lymphatic system (Shields, 1992) and the production and activity of NK cells (Bennett et al. 2003, Berk et. al 2001);
v) improved respiratory functioning, reduced possibility of pulmonary bacterial growth, (Fry, 1994) and reduced effects of bronchial asthma (Kimata, 2004(a)) and obstructive lung disease (Brutsche, Grossman & Muller, 2008).
vi) increased energy expenditure (10–15 min of laughter increases energy expenditure by approximately 50–170 kJ [10–40 kcal])(Buchowski, 2005), which could be of particular benefit to obese individuals or those with reduced mobility.

Aspects i, ii and iii would have been relevant primarily to the psychological state of the mother, which, would have had a direct effect on the health of both herself and the child/children in utero. The most important factor listed that was primarily physiological was the raised pain

threshold, which may have provided occasional limited relief from chronic pain that can occur in pregnancy; typically in the lumbar back and posterior pelvic regions (Ostgaard et al., 1991, Wu et al., 2004). The other factors relate primarily to reduced levels of anxiety, stress and depression and they are of significant importance. Depression during pregnancy has numerous documented negative repercussions such as inadequate weight gain, suicidal tendencies, deteriorating social functions, psychosis, and inadequate pre-natal care (Bonari, 2004; D'Alfonso et al., 2002; Marcus, 2009). Post-partum depression can decrease the level of infant care including breast-feeding (Hatton et al., 2005) and result in poor cognitive functioning, behavioral inhibition, and emotional maladjustment in infants and children (Carter et al., 2001; Pearlstein, et al., 2009; Sohr-Preston & Scaramella, 2006). As such, these negative outcomes could potentially have been reduced in mothers and infants as a result of humorous interactions. Similarly, pre-natal stress has been shown to cause spontaneous abortion, preterm labour, as well as malformations, growth-retardation (Huizink et al., 2003), cognitive impairments (Bergman et al., 2007; Laplante et al., 2004; Mulder et al., 2002), increased fearfulness (Bergman et al., 2007), and language deficits (Laplante et al., 2004) in offspring, and all these deleterious effects could potentially have been reduced by humour. The direct nature of the potential benefits of humour in situations involving stress and depression is implied by the fact that the parameters by which stress and depression are measured include intensity of smiling and presence or absence of laughter (eg: Bergman et al., 2007; Lovejoy et al., 2000). Though there do not appear to have been any studies focused on the role of humour during pregnancy, humour has been documented as playing a positive role in gynaecological/obstetric communication (Kabakian-Khasholian et al., 2000; Pizzini, 1991). Aspects iv (improved immune functioning) and v (improved respiratory functioning) and vi are perhaps of less significance than the aspects relating directly to mental health, but still had the potential to increase the chances of survival of both the parents and their offspring.

The previously cited aspects relating to social dynamics and structures include:

i) Pro-sociality, involving an increased ability to initiate, maintain and enhance interpersonal relationships (Smoski & Bachorowski, 2003; Salovey et. al 2000; Lefcourt, 2001).
ii) An increase in empathy (Hampes, 2001), intimacy (Hampes, 1994), and interpersonal trust (Hampes, 1999).

iii) Provision of “a means for interacting persons to alter, create and structure social relations” (Freedman, 1977 p.155).
iv) An increase in the size of social groups (Dunbar, 2017).
v) An increased ability to diffuse aggression (as per Bourdieu, 1984).

The importance of these social aspects during pregnancy is largely self-explanatory. Pregnancy was (and is) a critical time when both the mother and unborn child/children were at an increased level of risk. Individuals involved in humorous behaviour would have experienced enhanced social cohesion with other individuals and within groups, and the groups involved would have been of an increased size. Within this dynamic there was a better chance that adequate food and shelter could be provided and there would have been greater protection for the parents and their in utero children from outside threats. There would also have been the additional benefits of food sharing, communal child-care, and coalitional defense. This enhanced social dynamic and its resulting benefits would also have had a positive effect in relation to depression and stress (as per: Cobb, 1976; Elsenbruch, 2006).

Post-natal

In the immediate post-natal phase, humour may have decreased the negative effects of post-partum depression, which has already been discussed. It is of value to reiterate here that research has also shown that laughter increases levels of breast-milk melatonin in nursing mothers, and feeding infants milk with increased levels of melatonin reduces allergic responses (Kimata, 2007) and may also improve sleep and reduce colic (Engler et al., 2012). Research has shown that smiling (Field et al., 1983; Wolff, 1963) and imitation (Field et al., 1983; Meltzoff & Moore, 1977) occur spontaneously at birth, and smiling is produced socially within a few weeks (Emde & Koenig, 1969), while laughter emerges spontaneously in children as young as 17 days old (Kawakami et al., 2006), and is one of the first social vocalizations (Deacon, 1997). Similar behaviour and schedules of development have been observed in captive chimpanzees (Mizuno & Takeshita, 2002; Tomonaga et al., 2004), which indicates that it is appropriate to attribute the same capacity to hominins in the evolutionary phase in question. It is interesting to note that there is parity in imitative capacity at this early stage, while in contrast human adults demonstrate much greater imitative capacity than adult chimpanzees as has already been

discussed, and it is proposed that humorous interactions would have promoted the evolution of this ability in hominins.

Human infants can distinguish smiling at birth (Field et al., 1983), and smiling, laughter and humour are important aspects of infant directed communication (McGhee, 1979; Mireault et al. ; Reddy, 2001; Shultz, 1976). Tomonaga et al. (2004), note that in both human and chimpanzee infants, all interactions with others are emotionally based and Dissanayake's description of infant directed communication clearly evokes its comic nature: "undulant, high pitched patterned repetitive vocalizations … and exaggerated facial expressions, head movements and gestures" (2001 p.86). This description could as easily apply to a clown as to a parent, and Reddy has discussed the development of clowning in pre-verbal infants (2001, 1998). While communication with infants in the immediate post-natal period is typically not intended to be instructional, it still has the potential to communicate information (Brand et al, 2002) and it stimulates the use of specific communicative devices involving movements, facial expressions and vocalizations, as well as biological aspects associated with detection. It is notable that language is not listed as an element in Dissanayake's description of "babytalk", but regardless of this, it should be recognized that the "nonsense" vocalizations of modern humans have phonological, morphological, and syntactic characteristics related to the faculty of language (Soderstrom, 2007) that possibly would not have been present in the evolutionary phase under consideration.

The cognitive and emotional stimulation that would have occurred as a result of humorous communication with hominin infants in early childhood was of particular importance because it is during this phase that brain structures relating to specific behaviours developed, thus affecting the creation the functional structures that were present in adulthood (Duffy et al., 2004; Gao et al., 2009; Johnson, 2000; 2001). The role of significant cognitive/affective episodes such as those stimulated by humorous interactions are described by Scherer as being the cause of "strong synchronization of various organismic subsystems, particularly the various expressive channels, over a very brief period of time" (1994, p.181). Repetition of this type of "strong synchronization" would have served to strengthen specific neuronal pathways, in a process that is often summed up in the Hebbian notion: what fires together, wires together p. In addition to this, research has shown that laughter affects gene expression (Hayashi et al., 2005 and 2007). The Hayashi et al. 2005 study suggested that "laughter influences cell division and growth" (2005 p.65) and the Hayashi et al. 2007 study stated that "laughter influences the expression of many genes classified into immune responses, and may contribute to amelioration of postprandial blood glucose elevation through a modulation of NK cell activity caused by up-

regulation of relating genes" (2007, p.281). As such, it can be seen that humorous interactions would have had the potential to affect the functional dynamics of neural systems and gene expression (epigenetics), which could have had a broad range of ramifications relating to cognition, behaviour and general health. It is also likely that the stress reducing effects of humorous behaviour that were discussed earlier in regard to the mother, were also applicable to infants (directly and indirectly) and in the early post-natal phase this could have positively affected epigenetic development (Franklin et al., 2010; Jawahar et al., 2015).

In more general terms, the presence of humour in parent/child communication enhances bonding (Riem et al., 2012; Provine, 2001), and this would have helped to ensure survival into adulthood and thus, the possibility of reproduction. In a pre-linguistic evolutionary context, humour would have been an important tool in both educating and enculturating children because it communicated ideas relating to expected norms: a mechanism that points out the incongruous, points out the congruous by default[117]. The boundaries of social norms would have been mapped out by the identification of social abnormality and children who were better adapted to humorous communication would have been able to receive and communicate more information and thus would have benefited from a higher degree of social orientation. This is reflective of the pro-social nature of humour that have already been discussed (see pp.124-129) and the role of humour in defining identities (see pp.141-154), and is further supported by research demonstrating a positive correlation between humour and higher levels of social cohesion in children (eg: Bell et al., 1986; Chapman, 1973).

The same type of pedagogical dynamic would have applied to children learning about the physical environment. One documented example of this type of dynamic is the universal, humorous game of peek-a-boo (see p.80), which serves to help children grasp the concept of object permanence (Parrott & Gleitman, 1989; Schultz, 1976). The notion of the emergence of enhanced pedagogy from this type of behaviour in childhood is in agreement with Brune's assertion that "Neoteny has been considered the hallmark of human evolution, leading to persistent curiosity" (2000 p.301). It is proposed that humorous behaviour, especially in childhood, served an important pedagogical function, and its associated rewards had the

[117] Related to this, humorous interaction would also have enhanced the faculties of analogical thinking and causal reasoning (see. pp 118-121).

potential to cause an “upward spiral” similar to that described by Fredrickson and Joiner (2002) where positive mood enhanced learning, which enhanced positive mood etc.. This was of critical importance because it meant that hominin childhood learning had evolved into an autocatalytic domain-general process: children were self-motivated to learn about a potentially infinite number of things. This “upward spiral” is another example of the interrelated suite of positive feedback loops that have been discussed during the course of this thesis.

The presented scenario wherein humour and learning were strongly correlated was however, specific to the evolutionary context under consideration. The emergence of language introduced a far more direct and powerful method of communicating information that would have superceded the pedagogical effect of humour. It is proposed that at the point in ontological development where modern children begin to use language as their primary form of communication, the relationship between humour and learning becomes more complex and less direct, which is reflected in research showing modest or even negative correlations (eg: Owens & Hogan, 1983, Ziv, 1988). This is indicative of a parallel between phylogeny and ontogeny: in both cases the emergence of language signals the diminishing of humour’s pedagogical importance.

Summary

Humorous behaviour had the potential to yield substantial social, psychological and physiological benefits to pregnant hominin mothers and their unborn children, which would have increased the chances of producing healthy full-term offspring and having them survive the first years of life. During early stages of development, humour and its associated aspects of laughter and smiling would have enhanced parental bonding, and affected neural development and gene expression yielding benefits related to both cognition and general health. Humorous interactions in childhood would have helped to both educate and enculturate children and the associated rewards meant that humour functioned as an autocatalytic pedagogical system stimulating domain-general learning in a communicative format. In adaptive terms, parent/offspring relations involving humour would have produced children who were healthier, more communicatively and cognitively advanced, more socially and culturally integrated, and more likely to survive and reproduce. It more general terms, the preceding section shows how humour/humorous behaviour would have directly affected evolutionary dynamics, making hominins unique in the

fact that they could voluntarily transcend precedent dynamics based on aspects limited to genetics and environment.

9 Secondary ramifications of the general use of humour

In this section I will build on ideas and information from preceding sections and discuss specific possible ramifications of continued general humorous behaviour in hominins. The following section marks the point where evolutionary trajectory that has been proposed can be seen more clearly in social/behavioural terms, without losing focus on the key element of cognition. It marks a shift away from the more abstracted theoretical aspects and returns to the step-by-step approach that was adopted in the description of the eight stages of the emergence of humour. This makes the remainder of the thesis somewhat more approachable and self-explanatory, despite the fact that it involves some of the most complex notions, especially in the relation to the subject of language. The subjects under consideration are the general process of cumulative cultural evolution, and two of its aspects: the aesthetic faculty and language. It will be shown that the emergence of the requisite cognitive capacities and related behaviours were facilitated by humorous behaviour. The following sections make numerous references to ideas and information that have been discussed in preceding sections and there will be some page references provided to facilitate clear explanations to the reader, but to provide comprehensive page references would be unwieldy and should be unnecessary for anyone reading the thesis in its entirety.

9.1 Cumulative Cultural Evolution

In discussing the notion of cumulative cultural evolution, it is necessary to begin with a definition of culture itself, which is somewhat problematic due to the diversity of definitions and underlying criteria that exist (for reviews see Baldwin et al., 2006; Geertz, 1973; Kroeber & Kluckhorn, 1952). This is even more problematic when considering non-human culture (Galef, 1992), which is necessary in order to consider culture in the evolutionary framework in question. Perhaps the best known definition of culture is that of Tylor (1871): “that complex whole which includes

knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society." (cf. Asad, 1986 p.141), which is too narrow to be apply here. Laland and Janick's definition, "all group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information" (2006 p.542) is more suitable, but it puts sole emphasis on behaviour rather than the cognitive dynamics that underlie behaviour. Because of the emphasis on the cognitive aspect involved in the subject at hand it is better to apply the broader definition given by Hofstede: "the collective programming of the mind, which distinguishes the members of a category of people from those of another" (1984 p.389). While it could be claimed that it is a bit of a stretch to refer to patterns in neural activity as culture, it is these patterns that are responsible for the creation, expression, perception and interpretation of all aspects of culture, so these patterns are thus, inseparable from their external manifestations, which are more commonly thought of as culture.

Boyer (2000) recognizes the connection between cognition and culture in hominin evolution by referring to the modern human mind as the "cultural" mind, and says that the massive expansion of hominin culture that occurred in the transition from the Middle to the Upper Paleolithic (for a review see O Bar Yosef, 2002) can be explained in terms of "a newly acquired flexibility in mental representations" (2000 p.93). It is notable that this description could as easily apply to the shared domain-general cross-correlation between multiple schemata created through humorous interactions that has been described at several points in this thesis. Similarly, there are parallels between the dynamics of general humorous behaviour as they have been outlined, and the description given by Tennie et al. to illustrate the differences between the advancement of the cultures of humans and chimpanzees:

> …cultural human social learning is more oriented towards process than product and unique forms of human cooperation lead to active teaching, social motivations for conformity and normative sanctions against non-conformity. Together, these unique processes of social learning and cooperation lead to humans' unique form of cumulative cultural evolution" (2009, p. 2405).

Orienting towards process rather than product is indicative of the autotelic nature of humorous interaction, and within the proposed model humorous behaviour clearly involves active teaching, social motivations for conformity and normative sanctions against non-conformity.

Returning to definitions of culture, it can be seen that imitation, joint attention, and social learning are fundamental in the creation of culture (Heyes, 1993) because of their role in creating and sharing ideas, which has already been discussed in some detail. It was proposed earlier that the general use of humour would have created a situation where domain-general imitative behaviour directly yielded rewards and benefits (i.e. the process was autotelic), and thus over time, it would have qualitatively and quantitatively enhanced hominin imitative abilities, in part by increasing the chances that underlying genetic factors were replicated. It should be stressed that within this model humour-related imitative faculties were domain-general, which is significant because creation of human culture involves the cross-correlation of information between extrinsic domains, whereas patterns of social learning that create culture in non-humans tend to be domain-specific eg: feeding (Allen et al., 2013; Byrne, 2007) and foraging behaviour (DeWaal et al., 2013; Jaeggi et al., 2010; Reader et al., 2003). The role of innovation resulting from neophilia in relation to social learning was also discussed earlier and it was asserted that innovation drives social learning and, eventually, cumulative culture (Day et al., 2003; Kaufman & Kaufman, 2004; Lefebvre, 2000).

By considering the preceding it can be inferred that general humorous behaviour would have stimulated the accelerated development of the cognitive and behavioural prerequisites of the creation of culture. As such, the emergence of general humorous behaviour would have facilitated the emergence of bio-cultural evolutionary processes in addition to the existing purely biological ones. Humour would also have promoted biological aspects relating to physiology associated with modes of expression (vocalizations, gestures etc.), as well as in relation to any other genetic/genomic[118] aspects favoured by humorous behaviour. Aside from the role of sexual selection and the Baldwin Effect, which have already been discussed (see pp. 162-164), Jablonka and Lamb assert that recent data indicate "the genome is far more responsive to the environment than previously thought, and that not all transmissible variation is underlain by genetic differences" (2007 p.353) and they propose four types of inheritance: genetic, epigenetic, behavioural, and symbol-based "each of which can provide variations on which

[118] Genetics is the study of single genes and their role in the way traits or conditions are passed from one generation to the next. Genomics is a term that describes the study of all parts of an organism's genes.

natural selection will act" (2007 p.353). This emphasis on the importance of symbols is echoed by Wan and Chiu's definition of culture: ''culture consists of symbolic elements that members of a culture generally believe to be important to or characteristic of the culture'' (2009, p.80). As such, the previously discussed accelerated enhancement of symbolic competence caused by humorous interactions (see pp.137-141) is also of great importance when considering cultural evolution as a whole. Furthermore, the development of perceptual and motor skills related to gestures and vocalizations, the development of Theory of Mind and the capacity of analogical thought and causal reasoning, the increase in size of groups, and other cognitive, behavioural, and social advances that have been discussed can all be considered as relevant to promoting the creation and transmission of culture.

The term cumulative cultural evolution refers to the process by which culture is accumulated in specific populations over time, and the evolutionary path towards cumulative cultural evolution can be approximated in ontogenic terms by considering Tomasello and Carpenter's outline of developmental progression in early childhood development: "gaze following into joint attention, social manipulation into cooperative communication, group activity into collaboration, and social learning into instructed learning" (2007, p.121). As such, it can be seen that cumulative cultural evolution is a manifestation of hierarchically derived social learning. Cumulative cultural evolution is strongly evident in humans and is either absent in non-human animals (Tomasello, 1999) or extremely minimal (Whiten et al., 2003; Caldwell and Millen, 2009). Boyd and Richerson opine that cumulative cultural evolution is limited to humans, songbirds, and perhaps chimpanzees (Boyd & Richerson, 1996), but within songbird and chimpanzee populations such evolution is confined within specific domains with adaptive significance. In describing the dynamics of cumulative cultural evolution, Caldwell and Millen state that it "allows for the accumulation of modifications over time, involving a ratchet-like effect where successful modifications are maintained until they an be improved upon" (2008 p.3529) and regarding its origins, Boyd and Richerson conclude that "the capacities that allow the initial evolution of observational learning must evolve as a side effect of some other adaptive change" (1996 p.88). They go on to speculate that Theory of Mind could be considered as the "other adaptive change", and the proposed model has shown the positive effect humour had on the development of Theory of Mind. It is, however, perhaps more appropriate to simply see humour and the totality of its resulting cognitive and behavioural benefits as representing the "other adaptive change".

This can be illustrated more clearly by listing the specific factors relevant to such an evolutionary progression that have already been identified as resulting from humorous behaviour. The transition from the occasional, domain-specific social learning that can be seen in non-human animals to the ubiquitous, domain-general hierarchical social learning that is seen in humans would have been facilitated by the following factors already identified as resulting from humourous behaviour[119].

1) Improved communication skills and enhanced levels of cooperation.
2) Enhanced imitative ability.
3) An enhanced ability to form, retain, and recall memories.
4) The ability to cross-correlate information from multiple schemata (i.e. metacognition).
5) The creation of larger group sizes with greater social cohesion.
6) An enhanced capacity for analogical thought and causal reasoning.
7) An enhanced capacity for symbolic thought and communication.
8) The creation of individual and social identities and the ability to attribute mental states in others (i.e. Theory of Mind).
9) The operation of a suite of interrelated positive feedback loops that stimulated and sustained behaviour relating to the preceding factors.

The preceding list shows that the emergence and proliferation of humour represented an important step in the acceleration of cultural evolution and the creation of the modern human mind. Humorous behaviour and the ramifications of such behaviour were cultural in their essence in that the shared bodies of information that were translated into the creation of shared bodies of domain-general social capital[120]. The term "social capital" refers in a general sense to accumulated knowledge, behaviours and skills that can display cultural competence, and reflect and/or affect an individual's social status. Paldam (2000) has proposed that social capital can be divided up into three dynamic aspects: trust, networks, and cooperation[121] all of which were touched upon earlier in the discussion on the creation of identities (see pp.141-154). The role of

[119] For the purposes of précis the list that follows is not a comprehensive one but does cover the most relevant factors.
[120] It is acknowledged that the term "social capital" can be construed as implying an economic aspect, and that doing so introduces an historical element but within this thesis the term is applied in a broader sense where the aspect of "capital" is analogous.
[121] Paldam utilizes the common rather than specialized meanings of the specific terms "trust", "networks", and "co-operation" but describes the complex dynamics of their interrelated operation (2000).

humour as social capital can be seen by considering it in relation to the following statement by Bourdieu:

> Capital, which, in its objectified or embodied forms, takes time to accumulate and which, as a potential capacity to produce profits and to reproduce itself in identical or expanded form, contains a tendency to persist in its being, is a force inscribed in the objectivity of things so that everything is not equally possible or impossible. And the structure of the distribution of the different types and subtypes of capital at a given moment in time represents the immanent structure of the social world (2011 p.81).

It can be seen that information and symbolically representative expressions and related embodiments that were yielded directly and indirectly as a result of humorous behaviour conform to these criteria: they took time to accumulate, had a potential capacity to yield rewards and reproduce themselves in expanded form, etc. If one takes into account the proposed role of humour in the emergence of consciousness (see pp.157-158) in tandem with dynamics of reward it is possible to hypothesize that humour was the first example of consciously recognized reward in association with symbolic forms and, as such, it stimulated the emergence of domain-general social capital.

So it can be seen that humorous behaviour would have created and shared a body of social capital while stimulating neophilia in expanded social groups, and that would have resulted in the creation of diverse modes by which social capital could be created and exchanged[122]. If this overall dynamic is considered in terms of an evolutionary timeline, it may have coincided with the aforementioned Upper Paleolithic Revolution, which occurred approximately between 30,000 and 60,000 ya (Bar-Yosef, 1998; Klein & Edgar, 2002, Tattersall, 1995)[123], though others have argued that the advancement in culture that occurred was not as dramatic and suggest a more gradual shift (e.g. Hodgson, 2006; McBrearty & Brooks, 2000). Leakey has described the changes that occurred in relation to cognition:

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[122] This process will be outlined shortly in relation to aesthetics and language.
[123] This time frame approximately matches the previously mentioned one for the emergence of the (7R) allele of DRD4 gene.

> Unlike previous eras, when stasis dominated, innovation is now the essence of culture, with change being measured in millennia rather than hundreds of millennia. Known as the Upper Paleolithic Revolution, this collective archaeological signal is unmistakable evidence of the modern human mind at work (1984 pp.93-94).

Evidence for this cultural explosion can be seen in the archaeological record in artefacts such as tools, beads, paintings, figurines etc., as well as evidence of long distance trade, special organization within habitations, symbolic behaviour in association with burials etc. (for a summary see Bar-Yosuf, 2002).

In ascribing a key role to humorous behaviour in the evolutionary transition into the cultural it is necessary to address the possible criticism that this transition did not produce artefacts that appear to be overtly humorous in nature. I will begin to address this[124] by pointing out that the interpretation of an object as humorous is largely subjective and predicated on social norms as well as the specific circumstances (emotional and otherwise) relating to the situation in which the artefact was first created and/or presented. What was funny to individuals or groups at that time might not appear funny to us. It is also quite reasonable to believe that the gravitas of the academic tradition may have had the effect of transforming that which was once funny into something "sacred", and at the same time misattributing it with unintended symbolic significance. D'Azevedo sums the first point up well in relation to art: "Insofar as art is composed in a social setting and has a cultural content, this content can only be understood in specific cultural terms at given periods of time" (1958, p.703) but it can also be summed up by the phrase "you had to be there". An object could also have been initially intended to be comical, but subsequently have evolved other symbolic significance in hominin populations over time. Even if there were no evidence of comic expression at this time (and it will be shown that this is not the case), it is proposed that humour would have stimulated the cognitive, social and communicative development that was necessary for the cultural transition that occurred during the Middle/Upper Palaeolithic period, and as such related artefacts etc. should be considered to be products representative of the cultural elaboration of the underlying mechanism of humour.

[124] Further consideration of this question will be given later (see pp.196-197).

Barkow (1989) has proposed that culture is a system of socially transmitted information and that the emergence of modern human culture marked a transition from primate social dominance into human self-esteem and symbolic prestige. Within the proposed model, it can be seen how humour's contribution to the definition of self and other, enhancement of social cohesion and symbolic competence would have played a key role in such a transition. Similarly, in discussing key elements of the social intelligence hypothesis, Sterelny refers to "a feedback loop between human cultural and cognitive complexity that drives the elaboration of each" (2007 p.720). The role of feedback loops in association with the dynamics of humour has been consistently referenced in this thesis and it can be seen that within the evolutionary phase in question there would have been a humour-driven suite of interconnected feedback loops relating to cognition, communication and social structure and dynamics, which could also be thought of as a heterocatalytic system. Significantly, these feedback loops were partially socially and affectively mediated rather than purely adaptively mediated, which was a key aspect in the development of the analogical thought, and would have been similarly important in the development of an aesthetic faculty.

9.2 The aesthetic faculty

Imaginative and creative expression that emphasizes form over function can be seen in all human cultures (Deacon, 2006), and even though archaic societies often lack a word to denote "art" (Pasztory, 1996), such expressions still exist in these societies. The term art can refer to the act of creation of such expressions, it can refer to that which is created, and it can refer to the experiencing of such creations. As précis is of importance in this thesis, rather than consider the numerous extant theories on what consititutes "art" I will simply adopt Dutton's definition of art: "artifacts (sculptures, paintings and decorated objects, such as tools or the human body, and scores and texts considered as objects) and performances (dances, music, and the composition and recitation of stories)" (2009 pp.51-52). It is noteable, however, that while both humour and artistic expression appear in all cultures, the act of artistic creation does not display the same level of participation within its universality: in any given day the average person is far more likely to try to be funny than to try and produce a work of art. The greater ubiquity of humour suggests that it preceded art in evolutionary terms, and this is further supported by Bourdieu's notion of aesthetic perception summed up by Rosario and Collazzo as "a deciphering operation that is learned or socially acquired and may be conscious or

unconscious" (1981 p.74), which denies it is innate and implies a greater degree of social/cognitive complexity. There still remains the question however, is humour a form of art itself? Because if it is, it would constitute an aesthetic form that emerged from an affectively mediated reflex based on biologically predicated cognitive functioning (as has been outlined) rather than as a result of the deciphering operation that Bourdieu suggests.

It is proposed that it is reasonable and logical to classify humour as form of art: Charlie Chaplin and Robin Williams were as much artists as were Stravinsky and Miro. In support of this, many definitions of art have striking parallels with the proposed model of humour; from Plato's assertion that art is imitation[125] (Plato, 1974), to Tolstoy's definition "a means of union among men, joining them together in the same feelings" (1995 p.121), to Dissanayake's evolution-based description of art as a process where "ordinary reality becomes extraordinary by attention-getting, emotionally salient devices" (2017, p.143). In discussing the evolutionary origins of the aesthetic faculty (i.e. the faculty of creating and/or appreciating art) Deacon defines art by way of the following criteria: "(1) an extraction from direct instrumental communication; and (2) a duplicitous logic of representation: there is what it is or presents, and there is what it conveys only in some figurative form" (2006 p. 22). This can easily be re-interpreted as art is autotelic expression involving incongruity. Here, the definition of art parallels a description of humour, but without the prerequisite characteristics of positive emotional valence and a smiling/laughter response. Bearing this in mind, it should be considered possible that the earliest aesthetic forms were either humorous expressions that possessed and/or developed characteristics that stimulated interest/engagement beyond amusement, or were the results of the neophilic social behaviour that general humorous behaviour engendered. Later in the same paper Deacon adds another element: that art involves an "easily activated compulsion to treat objects or actions as signs (icons, indices, or symbols) for something beyond themselves" (2006 p.25). Again, this parallels humorous behaviour, which has already been shown in the proposed model to have involved novel reconfigurations of actions, object and ideas potentially involving displacement, and symbolic expression and interpretation.

While humour is the central topic under consideration, it is acknowledged that the emergence of the aesthetic impulse, much like broader issues relating to cognitive, communicative and social

[125] For more on the relationship between humour and imitation see pp.87-88 and pp.137-138.

evolution, must be considered in terms of other contributing factors. Scholars have noted many existing behaviours that would have been of importance in potential hominin aesthetic expressions including vocalizations (Miller, 2000(b)) and body decoration (Dutton, 2003; White, 1992) related to sexual selection, parent/infant communications (Dissanayake, 2001), vocalizations related to hunting related communication (Brown, 2000; Geist, 2013), and the creation and curation of tools (Chase & Dibble, 1987; Hodgson, 2011). These, however, are all domain-specific telic behaviours with specific adaptive value(s) and would have required an external factor (or factors) to cause them to evolve into impractical autotelic behaviours: domain-specific behaviours tend to remain domain-specific. Pinker and others have claimed that impractical autotelic behaviours such as art and music emerged as spandrels (eg: Donald, 2006; Pinker, 1999), and Davies comments "If art behaviors came to us as spandrels, they would not remain so; their occurrence in the usual manner would become normative because they would come to provide honest signals of fitness" (2010 p.335). If this view is accepted, it is possible that the aesthetic impulse may be considered to have been a spandrel resulting from humorous behaviour. Donald's ideas regarding the emergence of art also correspond with the proposed model in that he asserts, "art is an inevitable by-product of mimesis – a primordial, and truly human cognitive adaptation" (2006 p.14). Here, importance is placed on imitation, which has been shown to be a central component in the operation of humour (see pp.87-88 and 144-145).

The proposal that art emerged as a spandrel is come to in part because art, like humour, has been seen by some scholars as an autotelic behaviour lacking in notable adaptive benefits (eg: Pinker, 1997), despite a number of benefits yielded by artistic behaviour that have been documented in a modern context (eg: Črnčec et al., 2006; Routhieaux & Tansik, 1997; Stuckey & Nobel, 2010). In addition to this, aesthetic expression has a notable degree of positive correlation throughout history with mental and physical illness (for a review see Sandblom, 1992). While the adaptive benefits of art are up for debate (eg: Dissanayake, 2008), the greater ubiquity of humour indicates it to have been a more evolutionarily ancient behaviour, and it involved the cross-correlation and sharing of symbolic information in an autotelic manner thus facilitating the emergence of the aesthetic faculty. The Cognitive Fluidity model proposed by Mithen (1996) is in agreement with the importance of the cross-correlation of information in the emergence of the aesthetic faculty but the model lacks the crucial element of motivation, which is provided by the numerous rewards yielded by humour. Deacon indicates the importance of motivation in the emergence of the aesthetic faculty when he refers to "the likely possibility that

human cognitive and neural evolution includes a significant modification of typical mammalian motivational systems" (2006 p.26), though he offers no suggestions as to how this may have occurred or what it may have entailed.

It is the mapping of possible specific evolutionary pathways and their underlying causal mechanisms that separates theory from speculation. To that end it is worth considering what paths might have provided a bridge from humorous behaviour to aesthetic expression and appreciation. One possible path is that expressions that were initially humorous became ritualilized through repetition and thus evolved into aesthetic expressions[126]. It has been shown that rewards would have provided a drive to repeat a humorous expression, but there would also have been an entropic dynamic involved where the returns diminished with continued repetition. This type of dynamic in humour has been described by Rime (2009) and it shows that funniness eventually declines with continued repetition (Weisfeld, 1993[127]). Repetition has already been mentioned, and it is a frequently cited aspect of comic expression (eg: Molineux, 2014; Reddy, 2001). Repetition functions as an effective comic tool because it represents a break in the expected pattern of communication (it is not typical to witness the repetition of actions and vocalizations without practical reasons), but with continuation it tends to conform to expectation rather than the opposite: it becomes congruous rather than incongruous. This represents a process of habituation/ritualization and in evolutionary terms it would have created the potential for more complex cognitive/perceptual and social dynamics. The expression eventually becomes less humorous but can potentially possess other significance i.e. aesthetic qualities. Cori et al. (2016) have described similar cognitive/perceptual gradations relating to the processing of contrariety and irony in a Gestalt framework. In addition, a repeated humorous expression had the potential to be new to the observer of it, but not to the person expressing it. This would have been part of a ritualization process, and it was also significant in terms of classifying humour as a form of art. From the perspective of the individual creating the humorous expression, this dynamic meant that they no longer experienced the incongruity (surprise) but the expression could still potentially elicit a smiling/laughter response and thus, this type of humorous expression can be seen to fit the definition of a performance: "assumption

[126] It is acknowledged that a conundrum exists here if humorous expressions are considered be aesthetic in nature, but if this is the case the scenario helps to explain the evolution to other aesthetic forms.
[127] The origins of Weisman's observation are from Gelb & Zinkhan (1986).

of responsibility to an audience for the display of communication competence" (Olaniyan & Quason, 2007 p.384). In this way hominins expressing humour became performers for an audience rather than participants in a joint activity, and comic expressions would have become progressively more ritualized: birth of the artist. This type of performance is involved in the majority of infant-directed humour, and Dissanayake has proposed that mother-infant communication was the keystone in the emergence of what she calls "homo aestheticus" (2001(2) p.85). Though she recognizes aspects such as the intensity, contour, rhythm and duration of voice, as well as gesture and facial expression not necessarily predicated by language, her model explicitly assumes the presence of language and as a result, in comparison to the model proposed in this thesis, is more illustrative of an ontogenic process than a phylogenic one, or else assumes art to have emerged at a later point in evolutionary time than language. While this thesis is in agreement with numerous aspects of her model (eg: the ritualization of repeated behaviours) there is no valid reason to limit the type of interactions described to mothers/infant communication and discount the notion that similar communication occurred between adults.

An additional dynamic that would have been involved in the ritualization of humour is described by Girard's (1965) theory of mimetic desire[128], which asserts that it is possible for something to be desired by one individual simply because it is desired by somebody else, so the relationship between the subject and the object is not a direct one. In the scenario of a comic performance with an audience of two or more people, an individual who was not actually finding the performance funny could alter their behaviour because they desired to have the same experience as someone else who was enjoying the performance; to benefit from the same positive experience and so they would laugh/smile even though they didn't find it funny. This is one example of how non-Duchenne laughter and smiling may have evolved as social tools, and it can be seen that non-Duchenne laughter and smiling now contribute more to human conversation than their Duchenne counterparts (Mehu, 2011; Provine, 2004). The "mimetic desire" scenario is indicative of the potential of humorous behaviour to promote situations involving synchrony, which would have been relevant to the emergence of the aesthetic faculty

[128] It should be noted, however, that the humour example doesn't fit in with Girard's model entirely in that humour, unlike a physical object, can be shared without an element of diminishment, so no competition, violent or otherwise, results.

as manifested in the group activities of music and dance. With humour, the synchrony that was typically involved was the smiling and antiphonal laughter of the responders and as such, the synchronous behaviour was associated almost exclusively with responders rather than performers. It would however, also have been possible for individuals to create humour by synchronizing actions that were typically non-synchronous thus creating incongruity (eg: imitate someone in situ) and this type of humorous expression would have yielded rewards and benefits for the act of voluntarily creating synchrony. Launay et al. have noted, “Given that synchronisation is essentially mimicry involving temporally precise prediction of the movements of co-actors, it is likely to have similar, if not more pronounced effects on bonding” (2016 p.782). In essence, the benefits of mimicry (i.e. imitation) are proposed to have been magnified through synchrony and as such, group aesthetic activities like music and dance can be seen to have various adaptive benefits. Attribution of such benefits, however, fails to acknowledge an issue relevant to how and why such activities might have emerged. Namely that activities like music and dance involve sequences of sounds/gestures and a single sound (vocal or otherwise) or gesture does not constitute music/dance, and such sequences are unlikely to have emerged fully formed. This means that there must necessarily have been an interim phase where individuals and/or groups were inclined for some reason to create and enjoy singular sounds/gestures, and humorous behaviour would have provided just such an interim phase.

So it can be seen that humour may have acted as a catalyst for collective aesthetic behaviour, which would then have caused further social bonding, which would in turn have provided the long term impetus for continuation/proliferation despite the diminishing of rewards based purely on humorous response, caused by the process of ritualization. In this way these symbolically richer forms of expression could be established as elements of culture, and then, such ritualized forms could be expressed by individuals as well as collectives and continue to evolve to a point where they were potentially devoid of any humorous significance. They would, however, have retained adaptive benefits related to sexual selection derived from their humour-based roots the dynamics of which are summed up by Miller as “aesthetic displays play on the perceptual biases of receivers to attract attention, provoke excitement, and increase willingness to mate” (1998, p.96). In this way, humorous behaviour would have triggered the creation of voluntary, ritualized actions, gestures and vocalizations, which were the forerunners of music, dance and other aesthetic displays. Underlying this process were the initial behaviours that were generally recognizable (animal imitations, infant directed communication, gestural signals etc.), which

could be derived from a wide variety of domains, but humorous behaviour served to cross-correlate and communicate such information and provided the critical element of motivation.

So it can be seen that humorous behaviour had the potential to facilitate the emergence of aesthetic expression and appreciation. The process of ritualization that has been outlined also addresses a possible criticism that there is a divide between the arts and humour in relation to their emotional derivations and responses. It was asserted earlier that humour is predicated on a positive emotional valence and evokes mirth[129]. In contrast, other forms of art are derived from and can evoke, the full spectrum of emotion (for a summary see Rolls, 2017). This divide is largely explained by the process of divergence and evolution that would have occurred during and after the outlined process of ritualization, but it is also worth considering that humour had potential to have associations with a broad range of emotions as well, even if its functional dynamics did not require them. For example, as has been discussed, humour could have been used as a form of aggression as well as affiliation, or simply have involved a situation where one person's pain was another person's amusement. Humour involving negative and competitive emotions is observable in children at least as early as 8 months (Reddy, 2001) and such types of humour are common in modern humans (Kubie, 1971; Martin, 2010). If there was a humorous episode referring to an object or event that had associations with potential negative emotional valence, for example, when someone pretended to hit their head, the episode could initially be seen as humorous. With repetition, however, the humorous effect could be diminished and the potential negative emotional valence could be realized. The comic could become tragic. It would have been possible to have "angry-funny", "sad-funny", "confused-funny" etc. just as it is possible today, dark comedy is a well-established form (Styan, 1968) and these types of humour had the potential to become tragic/dramatic through the process of ritualization[130].

This dynamic would have served to parse activities, individuals and objects in collective experience into the categories of those that were appropriate to laughter and those that were

[129] It is acknowleged that humour can in some cases be seen to incorporate a variety of emotional content (there is dark humour, aggressive humour etc.), but it is asserted that other forms of artistic expression have the potential to encapsulate a broad spectrum, if not the total spectrum, of human emotion and the same cannot be said of humour.
[130] Before the establishment of (non-humorous) aesthetic expression as a norm, all forms of re-presentation would have been incongruous and thus, potentially comical.

not; a one-dimensional type of taboo. This can be seen to some degree as having provided an emotional equivalent to the parsing process outlined in the emergence of analogical thought (see pp. 118-121). The operation of humour would have recognized and shared the knowledge of such taboos and the degree to which, or circumstances within which, something could be laughed at would have provided further information defining the degree and boundaries of the taboo in question. All cultures and groups have subjects that are considered to be inappropriate for humour (Alford & Alford, 1981) and it is proposed that humour helped to identify and define networks of taboos and share this abstracted information within the group. So, at this early stage of human cultural evolution, it seems likely that humour would have defined taboos as much as taboos defined humour. Humour continues to have an involved relationship with taboos and still has the potential to define and evolve them (Bucaria & Barra, 2016).

In sum, within the proposed model, the path from humorous expression to general aesthetic expression involved the repetition of humorous expressions leading to their ritualization. This evolutionary sequence involved the incorporation of singular expressions that can occur in humour, as opposed to the more complex patterns of expressions required in other aesthetic expressions. One note is not a song, and one line is not a drawing, but a single expression can be funny: humour is the simplest art. This process would have developed shared expressions with potentially broad emotional and cognitive dynamics, and it is suggested that possible correlations with the development of analogical thought merit further study. This process would have developed the hominin faculty to create emotionally and symbolically diverse domain-general symbolic expressions imbued with social capital i.e. the aesthetic faculty.

Visual Art

Having established some of the basic evolutionary dynamics that might have allowed humorous behaviour to have facilitated the emergence of the aesthetic faculty it is worth giving further consideration the evolutionary dynamics that would have occurred in relation to specific aesthetic modes such as visual art. Visual art is of particular interest in an evolutionary framework because it created artefacts such as paintings, sculptures and instruments, that had the potential to survive, or partially survive, into the present. Some of the earliest examples of what might be considered to be visual art were created using red ochre (Hovers et al, 1993; Meyer et al., 2009) and hominin collection of ochre can be traced back 200-250 KYA (Roebroeks et al., 2012). Ground ochre pieces, ochre powder, or traces of ochre on grindstones

or stone tools have been found at sites such as the Blombos cave (100 KYA) in South Africa (Henshilwood et al., 2011) but significantly, no actual art from this time period has been discovered, only evidence that ochre was collected and presumably used in an indeterminate way. The earliest examples of actual cave art that have been discovered (at the time of writing) are the hand stencils in the Maros karsts of Sulawesi, which have a minimum date of 39.9 KYA (Aubert et al., 2014), though recent research has indicated that similar expressions in Spain may date back to at least 64.8 KYA (Hoffman et al., 2018). There has been speculation that the earlier ochre use may have involved body decoration (eg: Meyer et al., 2009; Watts, 2002), but if the aesthetic impulse emerged in the form of body decoration and then remained bound to that singular form alone for tens of thousands of years, why would it have eventually broadened it its scope? Other animals such as Bowerbirds have visual displays that have not broadened past the purpose of mate attraction, so even if one does consider such displays to be art (e.g. Endler, 2012), their uni-dimensionality becomes a defining aspect, making it a very specific type of art, with no reason to evolve beyond mate attraction. As such, without some faculty unique to hominins (i.e. humour), their use of body decoration in relation to mating would have led only to more use of body decoration in relation to mating: domain-specific behaviour remains domain-specific. Furthermore, the body decoration hypothesis may not be valid because ochre is equally likely to have been used by hominins for practical purposes such as protecting the skin from the sun (Rifkin et al., 2015), or as an adhesive or in the tanning of hides etc. (for a summary of possible uses see Roebroeks et al., 2012). If this were the case, ochre would have been a material present in the lives of hominins, but it was collected and used for practical (telic) purposes. If this were the case, how might the autotelic, artistic use of red ochre have emerged?

Any practical usage of red ochre would have involved manipulating it by hand. This raised the possibility that the image of a hand (or finger) might be accidentally produced in either outline or print. It is logical to surmise that the first handprints would have been accidental and later on have become voluntary. Support for this “accidental” mimetic origin of visual art can be seen in the fact that hand stencils are one of the earliest forms of human art (Aubert, 2014, Hoffman et al., 2018) and occurred in numerous disparate locations (eg: Aubert, 2014; David et al., 2013; Pike at al., 2012). Any initial accidental incidents would have necessarily been novel/incongruous occurrences resulting in the imitative representation of a part of the human form. As such, these representations were likely to have been seen as funny and thus, they would have been repeated and shared with others, who in turn, would have tried to imitate them in order to stimulate humour related rewards. Continued repetition would have ritualized the

behaviour as well as the social perception of the artefact, broadening the symbolic significance and associated emotional content as per the ritualization process already outlined. Put simply, it would have started as something funny, become something fun, and ended up as art.

Another trigger for this type of process may have been pareidolia[131] ("external stimuli triggering perception of non-existent entities" (Hogl, 2017)), which is most commonly associated with the phenomenon of perceiving bodily features (typically faces) in external phenomena (Liu et al., 2014; Takehashi, 2013). Higher levels of dopamine have been found to correlate with the propensity to find meaning, patterns, and significance where such do not exist (Belayachi et al., 2015; Leonhard & Brugger, 1998), so humorous individuals would necessarily have been more likely to perceive pareidolia[132]. The perception of pareidolia has also been associated with metaphorical thinking (Nowell, 2015), and is considered to be a contributing factor in the creation of Paleolithic art (Bednarik, 2013; Harrod, 2014; Malotki & Wallace, 2011; Nowell, 2017). Perhaps the oldest and most celebrated pareidolic object in relation to hominin evolution is the "Makapansgat pebble", a pebble with a natural pareidolic face (or possibly faces) found near an Australopithicine dwelling dating to approximately 2.6 MYA, which Oakley said "could be counted as one of the roots of art" (Dart, 1974 p.167) and Harrod described it as placing "curation, pareidolia and natural iconic figuration at the beginning of hominin symbolic behavior" (2014 p.136). While the date of the object is somewhat anomalous to the evolutionary timeline that has been discussed, within the proposed model, if humour had emerged at that point (if only in children), a found pareidolic object had the potential to be perceived, as novel/incongruous and therefore, funny. This is much the same today and proof can be seen in the fact that at the time of writing a Google image search for "pareidolia" is strongly dominated by humorous images (good for a laugh, please give it a try, the Jesus in a dog's butt is quite amazing). Once a pareidolic object was recognized (and possibly curated), it could then be shared with others, and there was the potential for attempts to replicate the object or its constituent features using the same or other media, which would represent the ritualization and iconization of the object as well as the process of its creation.

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[131] It is also possible to apply the broader term "apophenia".
[132] The hominin capacity for such behaviour is confirmed by Taubert et al's (2017) assertion "our results provide strong evidence that rhesus monkeys spontaneously perceive illusory faces on inanimate objects" (p.2507).

Pareidolian objects represent a good example of an item in the natural environment that hominins would have been more likely to perceive, acknowledge, and share due to its inherent qualities, bearing in mind the cognitive, behavioural, and social changes proposed to have been effected by general humorous behaviour. In relation to the emergence of visual art, the operation of humour would have yielded rewards and benefits for the sharing of perceptual incongruities in the external environment. As such, found objects such as pareidolia that had the potential to amuse were of importance. The key question was; was the object (or objects) in some way novel? Did the object(s) violate expected patterns of perception? There is supporting ontogenic evidence for this scenario in the fact that preferential interest in novel visual stimuli can be seen in human infants (Fantz, 1964). There is also an interesting inverse relationship worthy of consideration. In relation to any visual fields that were primarily arbitrary or random, any breaks in patterns (i.e. incongruities) would have, ironically, been manifested in form of patterns or symmetries. When patterns were representative of an incongruity, the drive to create and/or appreciate humour would have functioned as a pattern recognition system[133].

While complex natural symmetries exist in the environment in abundance (flowers, trees, animals etc.) more simplistic ones are rarer, as is pointed out by Hodgson:

> (a)lthough it is possible to find straight lines or geometric shapes in the natural environment, e.g. horizon lines, strata, celestial bodies, ripples, etc., these are the exception rather than the rule, as the natural world is dominated by apparent confusion (2006 p.58).

For example, in visually assessing an area with scattered stones of random shapes and sizes, humour related neophilia would have created an attraction to stones that were novel due to their observable physical attributes (eg: colour(s)) and/or configurations. A pareidolian stone is a good example, but stones remarkable for their unusual colour(s), symmetry or other observable physical attributes would also have been potentially attractive: only funny for a moment perhaps,

[133] The importance of humour's role in the emergence of analogical thought is evident again here, and further consideration regarding the possible co-evolution of the aesthetic faculty and the capacity for analogical thought is warranted.

but worthy of ritualization through curation and sharing. This process would have created value (i.e. cultural capital) in the curated/ritualized objects as well their cognitively abstracted characteristics. This would have had the potential to foster a desire to recreate such characteristics using external media, which may be what is seen in some of the earliest examples of symbolic expression such as geometric patterns seen in the Blomberg Caves (Henshilwood et al., 2002) and elsewhere (eg: Aubert, 2014). Repetition, which has been discussed in relation to humour at numerous points in this thesis, can also be seen in relation to palaeolithic geometric expressions (Hodgson, 2000) demonstrating another link between humour and the earliest forms of hominin art.

It is also notable that some examples of Paleolithic art used naturally occurring features of the rock as partial outlines for hominin and animal figures (Hodgson, 2008; White, 2003). Hodgson (2008) has proposed that the Paleolithic hominin mind was attenuated to detect hominin and animal figures and as such, the perception of pareidolia acted as a trigger for artistic expression and he suggests that this explains the emergence of visual art. The logic behind this theory is partially sound, but the theory is flawed in that it fails to account for the essential behavioural component of motivation. Just explaining that the capacity for a behaviour existed doesn't explain why such a behaviour might have emerged. The model proposed in this thesis incorporates Hodgson's ideas into a framework that provides an explanation for motivation as well as hierarchical development.

Detection of symmetry and patterns in visual input enables many animals to recognize and categorize the external world through visual input (Jitsumori & Delius, 2008), but in the more abstract sense, the identification of patterns is a complex operation: "Of all the visual tasks humans can perform, pattern recognition is arguably the most computationally difficult" (Olshausen et al., 1993 p.4700). Activities such as tool making would also have played a role in this, as hominin perceptual/cognitive abilities related to patterns would have been stimulated and evolved by the creation (and curation) of lithic objects such as weapons and tools (Hodgson, 2006; 2009), which were of evident adaptive significance. In relation to a possible timeline, tool production began to appear approximately 2.5 MYA (Panger et al., 2002; Susman, 1994) and the advancement of the degree of symmetry in tool making has been considered to correlate with intelligence levels (Saragusti et al., 1998). Significantly, the creation of tools would have involved the interfacing of visual and visuo-motor pathways so a cognitive/behavioural link between perception and creation of symmetry and patterns was developing that could have

been manifested in the cognitive/perceptual dynamics of humour. These abilities, however, appear to have not translated into a general capacity for symbolic expression for another 1.5 million years so it is difficult to see a direct causal link with artistic expression. In relation to this, Hodgson has proposed that when visual symbolic expression emerged, it involved "a self-generating feedback loop without the need for any extraneous reward because, as we have seen, producing marks of this kind is self-rewarding by way of, what I would argue, are the various dynamics contained in early visual cortex" (2006 p.60). This again brings up the importance of an autotelic mechanism and represents a feedback loop similar to those outlined in relation to humour implying a direct connection between the two. In cognitive/neurological terms, what fired together, wired together, and after the process of ritualization, Hodgson's proposed feedback loop would have had the potential to function separately from any humorous dynamic, and it would have been reinforced by the level of cultural currency of the artefact and its creation. The dynamics that have been outlined show a causal evolutionary sequence that helps to explain the rapid changes in symbolic/aesthetic expression that occurred in the "upper Paleolithic revolution", which followed a period of 1.5 million years involving very little change. They also provide a picture of how humorous behaviour combined with existing ecological factors to produce the cognitively and emotionally rich autotelic system that was required for the creation and appreciation of visual art.

Within the proposed model, the dynamics underlying the creation, perception and social aspects of visual symbolic expression would have evolved past the boundaries of the strictly humorous and involved broader emotional and cognitive elements. If this hypothesis is correct it should be possible to see traces of humour in prehistoric art, and this is indeed the case. The comic elements of prehistoric art have been noted by Ollins-Alpert and Vigier (1992), Bahn (1998), and Caron (2002), and in describing rock engravings from the Jebel Ideid, Anati opined, "the artist who drew this strange scene had a certain amount of sense of humour." (1956 p.7). There is some indication that the emotional valence involved in the creation of prehistoric art was positive, and thus conducive to humour, in that there is a marked lack of aggression in its content[134] (Curtis, 2007; Trovik, 2010). It is also notable that many prehistoric figures/figurines

[134] I acknowledge that humour can involve aggression, but in general terms, a lack of aggression is indicative of a positive emotional valence, which is a precondition of humour as it is defined in this thesis.

have comically exaggerated and distorted physical features, with emphasis on oversized sexual organs (Bahn, 1998; Gvozdover, 1989; Mcdermott, 1996). Such features are typically interpreted as being the product of expression related to sexuality and/or religion (eg: Gvozdover, 1989; Nelson, 1990), but that is speculative, and in either case should not preclude the idea that such expressions were initially humorous in nature. It is not unreasonable to believe that the depiction of a figure with a massive vagina and enormous breasts and buttocks could have been intended to express simple comic mockery (as per Bahn, 1998) as imitation and exaggeration are common aspects of humorous expression. Another example of this type of interpretation can be seen in relation to numerous examples of paleolithic hand stencils that were frequently contorted to form unusual patterns, some appearing to have missing, partly missing, or distorted fingers (Walsh, 1979 p. p.33). The tendency to in academic studies to attribute religious significance to qualities in paleolithic art is reflected by the fact that it has been suggested that missing fingers are the results of religious sacrifice (McCauley et al., 2018) and it is proposed that the hominin desire to create novelty is far more likely to have been the culprit.

The interpretation of such artefacts as "sacred" is just that; an interpretation, and it is reasonable to consider grotesque interpretations to have been comical in origin rather than sacred. Potentially, these types of figures were intended to be forms of amusing mockery, and the attribution of "sacred" is either inaccurate or was only the result of subsequent ritualization. Support for this idea can be found in the "Cambridge Illustrated History of Prehistoric Art" (1998) where it is proposed that it is possible to interpret humorous intent in works of prehistoric art. It is correctly pointed out that without the correct context, comic value is largely lost. The author goes on to note that humorous intent can be implied by "exaggeration, inversion, satirical caricature, the grotesque/monstrous, scatology …sexuality…and need to laugh at the misfortune of others" (Bahn, 1998 p.206). He cites examples such as a bas relief from the Roc de Sers site of a man being chased by a bison (c. 20 KYA), numerous instances of anthropomorphism, and an ice-age cave painting from Le Portel that shows the outline of a man, using an existing stalagmite emerging from the cave wall to represent the mans penis[135], complete with a red dot on the end for emphasis. Regarding the Le Portel image he adds, "most scholars assume that the Portel figure is a bit of fun" (Bahn, 1998 p. 209), and there is another

[135] This is another example of the use of pareidolia as per Hodgson (2008).

image known as “Laussel’s Priapus” that uses a similar technique (Angulo & Garcia-Diez, 2009) as well as a cuttlefish fossil that was curated in the Late Aucheulian in Erfoud, Morocco, that distinctly resembles a human penis (Bednarik, 2009)[136]. In sum, the comic aspects of visual art are difficult to ascertain because of their subjective and contextual nature but prehistoric art frequently displays features that could easily be interpreted as comic, but have not been previously perceived as such due to the nature of academic tradition. It is proposed that a cloud of gravitas may have served to obscure the vision of researchers, and figures such as the Venus of Hohle Falls were originally intended to be comical rather than sacred.

In sum, it can be seen that humorous behaviour provided a cognitive, behavioural and social framework, and cognitive/perceptual dynamics that facilitated the emergence of visual artistic expression and appreciation. Accidental visual expressions, pareidolic objects and objects with other perceivable incongruities in their physical attributes would have all been important in this. Through the process of ritualization and enculturation that has been outlined, expressions using visual media that were initially humorous in nature were imbued with broader symbolic and emotional significance as well as a degree of cultural capital while maintaining their autotelic aspect.

Music

The possible origins of music have been the subject of much speculation (eg: Brown, 2007; McDermott & Hauser, 2005; Mithen, 2005, 2008; Wallin et al., 2001). A comprehensive review of the literature is not possible within this thesis but different theories will be discussed during the course of this section. The general process and dynamics that were just outlined in relation to visual art, can also be applied to the emergence of music. The same general process and cognitive, psychological, and social dynamics, but related to audio rather than visual information[137]. As such, the emergence of music would have involved interplay between humorous behaviour and existing ecological factors[138] relating to the creation and/or

[136] Bednarik has also noted a cuttlefish fossil from the Late Aucheulian of Erfoud, Morocco, resembling a human penis - Bednarik, R.G., 2009. The global context of Lower Palaeolithic Indian palaeoart. *Man and Environment*, *34*(2), pp.1-16.
[137] The role of audio pareidolia may also be an example of this.
[138] For a summary of contributing ecological/biological factors see Fitch 2006.

appreciation of sound[139]. This process is proposed to have occurred roughly as follows[140]. An individual produced a sound or a combination of sounds that was/were perceived as incongruous in relation to expectation, and thus stimulated a smiling/laughter response in others. The incongruity had the potential to occur in relation to the sound's constituent elements and/or configuration and/or context. This would have resulted in a drive to repeat these audio expressions (with possible variations) in order to obtain further rewards associated with humour. Continuance of this behaviour would have ritualized both the process and the products (and their cognitively abstracted notions) for the creator(s) and the observer(s), broadening the associated emotional, symbolic and social significance. Over time, this would have created a body of sounds and patterns of those sounds with shared symbolic significance imbued with cultural currency separate from any humorous associations. Support for this scenario can be found in the positive correlation that exists between smiling/laughter and music acquisition in childhood development (Gerry et al., 2012; Trainor et al., 2012). Once again, it started off as funny, continued as fun, and ended up as art.

In considering the role of humour in the emergence of music it is significant that the vocalization of laughter was central to the operation of humour, and the role of antiphonal laughter in creating social cohesion and increasing group size has already been discussed (see pp.81-83). In neurological terms, laughter activates the supplemental motor area of the brain, which is associated with song production and speech (Wattendorf et al. 2012), and Dunbar has pointed out that

> ...singing shares with laughter and speech two important features, namely segmentation and breath control. Segmentation is important for the syntactical structuring of long sentences, but breath control is crucial in that it makes possible the long exhalations on which speech depends for its fluency (2016, p.2).

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[139] Peretz 2006 notes: "Paradoxically, the musical capacity appears to be fully developed in only a minority of humans who can make music".

[140] The process that is outlined in the section that follows is a theoretical one based on a logically plausible hierarchical progression based on a diversity of relevant information.

Laughter is more evolutionarily ancient than speech or music[141], and as such, it is logical that it would have served to help evolve the perceptual/motor elements that were required for singing and speech to emerge. In relation to this, it is important to recognize that laughter is not a singular vocalization but exhibits variety and complexity (for a review see Huber & Ruch, 2007), and variations can serve different communicative purposes (e.g. signaling mood, expressing affiliation, modification of the meaning of concurrent communication etc.) (Coser, 1959; Provine, 1996). Monkeys and apes are able to produce a variety of context-specific vocalizations in a variety of situations (Clay & Zuberbuhler, 2009; Marler & Hobbet, 1975; Taglialatela et al. 2003), which likely involve a broader range of vocal expressions and related motor skills than various types of laughter. The production of such domain-specific telic vocalizations has not, however, led to the emergence of music in any of these species. Music does not occur simply because an animal has the requisite vocal ability to sing (or the physical capacity to produce music) so the critical factor(s) involved must necessarily lie elsewhere.

One critical factor may have been the autotelic aspect that music shares with humour (McDermott & Hauser, 2005): musical expression occurs for the sake of itself rather than to achieve any specific extrinsic goals. Related to this it has been observed that music (including singing) stimulates dopamine release in humans (Chanda & Levitin, 2013; Menon & Levitin, 2005; Salimpoor et al., 2011), and at the same time increases the sense of belonging or social bonding (Pearce et al., 2015, 2016; Weinstein et al., 2016). Conversely, vocalizing in chimpanzees does not stimulate endorphin release (Raghanti et al., 2016) and only in rare cases in captivity do chimpanzees develop novel vocalizations (Hopkins et al., 2007). Interestingly, birdsong stimulates dopamine release in many birds (for a review see Simonyan et al., 2012) and it is thought that the dopaminergic system is involved in the modulation of their social-context-dependent song production and song learning (Jarvis et al., 1998; Hessler & Doupe, 1999; Yanagihara & Hessler, 2006). Birdsong is a learned and complex social behaviour, but it does not involve the rational organization of discrete sound intervals and there has been some debate as to whether or not it should be considered as music/musical (eg: Araya-Salas, 2012; Fitch, 2006; Rothenberg et al., 2014; Taylor, 2017). Regardless of this issue, it is evident that bird song is analogous, not homologous, to human song as there is no

[141] Fitch notes that birdsong is analogous rather than homologous, and though bi-manual drumming in African higher apes is representative of a homology it is not sufficient to claim such species to be substantially musical.

evidence suggesting any learning of complex vocalizations in nonhuman primates (Janik & Slater, 1997). The relationship between music and dopamine production does, however, need to be put into some perspective. Salimpoor et al. (2011) point out that while music stimulates dopamine release in humans, there is substantial variability in this correlation, and in contrast with humour there is a negative correlation with novelty (Salimpoor et al., 2013), which suggests a higher degree of social, as opposed to cognitive, mediation of reward. This dynamic is in keeping with the proposed model, in that humorous behaviour would have been the initial stimulus for autotelic novel auditory events, which would then have been repeated, ritualized and thus, "musicalized". The element of neophilia (and related creativity) in humour would have been an important one in relation to the emergence of musical behaviour because it would have stimulated the creation of novel vocalizations as well as novel sounds through the use of (novel) external media. Hominin humorous expressions could also have involved displacement of existing sounds from their original telic contexts: making a sound at an incongruous time so it was funny. The sounds and patterns of sounds that were best adapted to the existing biological/neurological constraints (for a review see Peretz, 2006) would have been gradually selected over time, but it was the tendency towards neophilia and the desire to create humorous sounds that would have allowed the requisite input for such a selection process to occur. The previously outlined process of ritualization would have imbued the expression of organized sounds with cultural capital, and fostered a desire to create and appreciate the organized expression of sound(s). This process of ritualization and enculturation, would have evolved the dynamics underlying the creation and expression of organized sound(s) beyond the cognitive and emotional boundaries of the strictly humorous, and allowed for broader cognitive and emotional elements.

Support for the preceding can be seen by looking at onotogenic parallels. The ability to detect the constituent qualities of music begins early in infant development but does not reach adult levels until about the age of seven (Trainor & Corrigal, 2010), thus displaying a much slower rate of ontogenic development than humour. The acquisition of the musical faculty is largely a culturally mediated process (Clayton, 2009; Hannon & Trainor, 2007; Hennion, 2003) but does have universal roots such as the prosodic and rhythmic elements of "motherese" (Balter, 2004; Parncutt, 2009). These roots, and much of the enculturated musical development that children experience typically involves the use of humorous elements (Arculus, 2011; Leblanc et al., 1992) and children "prefer music that they consider humorous" (Arculus, 2011 p.40). In the case of motherese, the musicality that occurs could be accurately described as the humorous

manipulation of sound intended to engage/amuse rather than actually being an intentional presentation of music. This is supported by the fact that the sounds produced constitute one aspect of a total audio/visual comic interaction that involves smiling, laughing and exaggerated facial expressions etc. (Dissanayake, 2004). Essentially, musical development in ontogenic terms is another example of a process that starts as funny, becomes fun, and ends up as art. The idea of this type of progression is also supported by the fact that non-human primates have a dislike for music (McDermott & Hauser, 2007), which suggests that in evolutionary terms there must have been some type of intermediate stage. The simplicity and prevalence of comic tools in vocal/non-verbal motherese does indicate that motherese might give some sense of what the earliest musical expressions were like, but only to a limited degree. The dynamics involved in parent/infant interactions are necessarily more muted than comic expressions that develop within rough and tumble play and there would likely also have been familiar sounds that were displaced from their original telic context, such as hunting signals and/or animal imitations.

As with visual art, the process of ritualization and enculturation would have evolved the dynamics underlying the creation and expression of organized sound(s) beyond the cognitive and emotional boundaries of the strictly humorous, and allowed for broader cognitive and emotional elements in its creation and appreciation that were imbued with cultural capital. Humour, visual art, music and other forms of aesthetic expression all served to both create and reflect cultural identities and dynamics. Aesthetic forms that emerged and involved temporally mediated expression (i.e. performance) would necessarily have involved a high degree of overlap and were likely indistinguishable as specific activities: movements would have accompanied the expression of sound. Over time, the cognitive abstraction of constituent elements would have gradually yielded more specificity. Humorous expression, as the initial source, would have involved elements of musicality, dance, puppetry (using gestures, objects or shadows), mimicry etc. and elements that were socially selected would then gradually attain a specific identity and cultural value and continue to evolve on an independent trajectory[142]. Temporally mediated performance involving multiple expressions would also have been of importance because it would have involved intrinsic patterns. If one sound or action is created

[142] Consideration of the emergence of dance has not been given due to the necessary degree of précis required in this thesis, but it is acknowledged that a substantial level of integration of music and dance likely occurred in the evolutionary period in question and a similar dynamic in relation to humour would have been involved. Higher levels of arousal associated with early humour are also relevant in this regard.

after another, the significance of that sound/action is predicated by the preceding one(s). If, for example, a high-pitched sound is vocalized, repeating that sound has one effect and contrasting it with a very low sound has another. Repeating the same phoneme ten times in a row would create a specific effect, and three high pitched vocalizations followed by one low pitched vocalization would create yet another effect. Essentially, performance involves sequences and each expression creates a level of expectation of what is going to be expressed next. This has the potential to create a proto-narrative structure because the sequence of expressions is being dictated by a simplistic syntax, which is mediated by a variety of perceptual, cognitive, affective, social and cultural factors. This type of dynamic is easily observable in drumming on a single object; the rhythm, speed, volume etc. can all be modulated to create perceptible patterns. This is also a particularly relevant example in that bi-manual drumming has been observed in higher apes (gorillas, chimpanzees and bonobos) (Arcadi et al., 1998; De Waal, 1988; Fitch, 2005) and Fitch has proposed that ape drumming represents a possible homologue to instrumental music (2005), though the aforementioned fact that music does not stimulate dopamine production in apes suggests that such drumming typically has a telic aspect.

Similar dynamics are also a central element of clowning in my own professional experience, and they have also been described well by Davison (2013) and Bouissac (2015). Other examples can be seen in the syntax (Valerio et al., 2006) and implicit narrative in musical structure (Maus, 1991), the "rule of three" in stand-up comedy (Double, 2013; Kinde, 2009), as well as the more general notion of comic timing (Attardo & Pickering, 2011). These dynamics can display complexity and function without the requirement of language. There would also have been mediation of these dynamics by the cultural norms of performance: what had been performed in the past partially determined what was expected later. There would have also been many other possible variants such as correlating or contrasting combinations of pitch and phoneme, or gestures and vocalizations e.g. looking big and using a tiny voice. Such variants may have been experienced accidentally at first, but with repetition, recognizable patterns would have emerged and eventually these became parts of consciously designed expressions intended to maximize rewards[143].

[143] The ramifications of these types of developments in relation to language will be explored in the following chapter.

Summary

It is proposed that continued general humorous behaviour in hominins would have enhanced numerous perceptual/motor, cognitive and social/behavioural factors that contributed to the emergence of the aesthetic faculty. These factors included but were not limited to imitation, joint attention, memory, analogical thought, symbolic competence, Theory of Mind, meta-cognition, neophilia, creativity, increase in group sizes, increased social cohesion and the development of perceptual and motor skills related to communicative expression. This proposed humour-driven system would have been domain-general, autocatalytic, and autotelic. Within the framework of existing biological constraints and ecology, humorous behaviour would have stimulated the autotelic creation, performance and repetition of different audio, visual, and gestural expressions as well as the perception, creation, and curation of symmetries and patterns in extrinsic media. Through repetition of both creation and perception, these objects and performances became ritualized and enculturated, which gave them broader emotional and symbolic significance and imbued them with cultural currency potentially independent from humorous association. The totality of these capacities of expression and appreciation constituted the aesthetic faculty and any specific products that resulted from these capacities can be referred to as art. This process would have been a hierarchical one and would have accumulated culture in specific populations over time i.e. it was a constituent of cumulative cultural evolution.

This process greatly raised the importance of bio-cultural evolutionary processes in hominins in relation to the purely biological ones. In communicative terms the development of temporally mediated forms of artistic expression, including humour, introduced cross-correlation of performance elements in situ involving simple, syntactic narrative structure, and stimulated the development of constituent elements of language such as phonemes and morphemes (see pp.211-216). In broader evolutionary terms, the proposed model presents a biologically rooted hierarchical progression involving a logical causal sequence, and thus explains how the emergence of the multiple modes of autotelic expression and appreciation that comprise the human aesthetic faculty may have emerged in both cognitive and behavioural terms. The preceding shows a progression towards the development of aspects that could have contributed to the emergence of language, which will now be considered in some detail.

10 The role of humour in the emergence of language

It has already been mentioned that humour, music and speech share the common ground of vocalizations and that laughter is more evolutionarily ancient than either music or speech. Humour typically involves vocalization in the form of laughter, but can also involve non-linguistic vocalizations in its expressions as well. Dunbar has pointed out the fact that singing shares with laughter the fact that we can sing with or without words (2016, p.215) and he considers both to have been factors in the emergence of language. Dunbar is not alone in making a connection between music and language; there has been some positive speculation in this regard (eg: Fitch, 2006), which is sometimes referred to as the "musilanguage" hypothesis[144] (eg: Botha, 2009; Brown, 2001; Mithen, 2005). One of the problems with this hypothesis relates to the issue of particulation in expressions. As has been discussed, music deals with temporal sequences/patterns whereas humour can involve single particulated expressions and thus, the voluntary configuration of those expressions. The development of a complex hierarchical system such as language would have required the cognitive identification, isolation, and abstraction of singular elements. This is exactly what would have occurred in the processing of humour, and the role of the phoneme was already touched upon. In contrast, music would have involved holistic collections of sounds, which may have communicated information, but this system did not demand any cognitive/communicative particulation of its elements beyond the intrinsic qualities of sounds themselves. The idea that language evolved directly from music is also problematic for a number of other reasons including the lack of related neophilia, rewards and benefits associated with music in comparison to language, which has been discussed. In addition to this, primitive musical forms are typically seen to involve chorusing (Merker, 2000), which is a synchronous form of expression that lacks the role asymmetry necessary for one person to convey information to another. Music involves the integration of parts whereas speech involves the alternation of parts (Brown, 2007) and "(a)lternation tends to be favored by dyads, which is the typical social arrangement of human speech" (Brown, 2007 p.17). There is also the question, if speech is the child of music, why do they tend to exist in very separate domains?

[144] To quote Brown, the Musilanguage Hypothesis proposes that that "music and language are homologous functions that evolved from a common ancestor that embodied their shared features" (2001 p.372).

While speech and music have a common prosodic component (Wennerstrom, 2001), it would be very unusual, (i.e. odd, amusing or disturbing) if someone you were speaking to started singing in the middle of a sentence, whereas humour, smiling and laughter are thoroughly integrated in speech (Nwokah et al, 1999; Provine, 1993). That said, music and dance, in conjunction with humour, could all have contributed an element of narrative structure in communication as well as non-verbal communicative elements (related to proxemics, kinesics (movement), vocalics (paralanguage) and chronemics) that are beyond the scope of this thesis, but may have contributed to the evolution of hominin communicative abilities that resulted in language.

Motherese has also been proposed to have had a central role in the emergence of language (Falk, 2004), but Bickerton makes a valid criticism of this proposal pointing out that there was no need for such sounds to have evolved into anything more complex: "(w)ouldn't meaningless sounds that were pleasing (for reassurance) or alarming (for warnings) and simply stayed that way done equally well?" (2009, p.71). Again, it is reiterated that domain specific activities tend to remain domain specific, and telic activities do not evolve their telos. That said, the role of humour within motherese is worth consideration and has already been briefly discussed (see pp. 201-202).

In more general terms, there are a number of problems associated with developing theories on the origin of language that should be addressed before going any further, and these are summed up well by Fauconnier and Turner:

> "There are many problems besetting theories of the origin of language. These problems include the absence of intermediate stages in the appearance of language, the absence of existing languages more rudimentary than others, the appeal to some extraordinary genetic event unlike any other we know of, and the difficulty of finding a defensible story of adaptation" (2008 p.1).

The proposed model presents a gradualist picture that dispels the need for an "extraordinary genetic event"[145], and the issues of intermediate stages in the appearance of language, the absence of existing languages more rudimentary than others, and the difficulty of finding a defensible story of adaptation will now be addressed by way of a review of the general relationships between humour and language as well as an examination of humour's possible role in the evolution of the five domains of language (phonemes, morphemes, syntax, semantics and pragmatics).

10.1 Humour in relation to definitions of language

There are several definitions of language that, if taken literally, would qualify humorous communication as representing a form of language in itself. Examples of these include: "Language is nothing but a set of human habits, the purpose of which is to give expression to thoughts and feelings, and especially to impart them to others" (Jesperson, 2003 p.1) and "Language in its widest sense means the sum total of such signs of our thoughts and feelings as are capable of external perception and as could be produced and repeated at will" (Gardiner, 1932 p.32). Both these definitions are broad in nature and no claim is being made that hominin humorous communication at the point in evolution being discussed should be considered to have constituted a language, but the fact that these definitions can be applied to pre-linguistic humour is indicative of the existence of profound parallels between language and humour. Pre-linguistic hominin humour would have involved the organization of information (by way of cognitive cross-correlation of information across schemata), as well as communication (by way of expression/perception/cognition). Bearing this in mind the definition of language and the evolutionary dynamic proposed by Logan (1995) are particularly relevant. The definition Logan gives for language is: language = communication + informatics (1995, 2000). Informatics in a general sense refers to the storage, organization and processing of information and in cognitive terms this can be seen as "internal information processing mechanisms and natural intelligence of the brain" (Wang, 2002 p.34). Once again, the definition is a very general one. All systems of animal communication have underlying neural mechanisms, which means they all possess informatic elements as well as communicative ones, and thus, by Logan's definition can be considered to be languages. Obviously, this is not what Logan intended to imply, and he does

[145] This gradualist picture does not, however, completely discount the role of genetically based changes such as the emergence of the 7R allele of the DRD4 gene which has been discussed.

go on to assign some importance to semantics and syntax, but once again, the important parallels between pre-linguistic humour and language are made evident. Logan presents this definition as part of a broader hypothesis on the evolution of language(s) within which he proposes "an evolutionary chain of languages with each new language emerging from the previous form(s) of language as a bifurcation to a new level of order à la Prigogine[146] in response to an information overload that the previous set of languages could not handle" (2006 p.1). Essentially, he is saying that evolving social and ecological dynamics involved in hominin/human existence created an escalating set of informational demands and new languages emerged to deal with the required level of information processing. This is similar to the model proposed in this thesis in that it shows an integrated, hierarchical progression, but the model in this thesis is based on logical causal chains created by a autocatalytic, hierarchical system: it shows how specific cognitive/communicative processes/dynamics would have resulted in novel forms.

Logan, like many others (eg: Aitchison, 1996; Hockett & Hockett, 1960), proposed that speech was the first form of language, though there has also been support for the idea of a gestural origin (eg: Armstrong & Wilcox, 2007, Studdert-Kennedy & Goldstein, 2003). As both vocalizations and gestures would have been used in humorous expressions, either scenario or a combination of both, is theoretically feasible within the proposed model. It has already been asserted that hominin humour should not be considered to have been a language, but in relation to Logan's framework, hominin humour can be seen to have represented an evolutionarily precedent co-dependent system of informatics and communication. It would have involved the cognitive organization/re-organization of information, the communication of that information, the retention of such information within shared bodies of information, and the drive to repeat its expression. As such, the proposed model addresses the aforementioned issues of determining intermediate stages in the appearance of language, and the absence of existing languages more rudimentary than others.

To recap, humour in hominins was an affectively mediated cognitive/communicative system predicated on the simple binary of incongruity between expectation versus perception and/or

[146] In relation to Prigogine it is possible to see the hierarchical/heterarchical progression outlined in this thesis as a self organizing system dependant on biological, behavioural and ecological factors.

cognitive correlation with previous humorous experience. This system yielded numerous adaptive benefits and was driven by rewards, which were functionally manifested into a suite of positive feedback loops. Cognitively, humour functioned as a rudimentary "break in pattern" recognition system, which, by default, served to identify patterns and facilitate the emergence and operation of analogical thought. Over time, humorous behaviour would have created and shared bodies of abstracted knowledge comprised of information cross-correlated across schemata. These shared bodies of social knowledge, and the means by which they were shared, would have been imbued with social capital. Continued general use of humour would have led to a hierarchical accumulation of knowledge and enhanced the ability to cross-correlate and conceptualize abstracted information and then to communicate the resulting novel concepts. This generative, hierarchical scenario would have created the type of information overload that Logan describes because without a formal shared symbolic system of communication, the potential for expression would have been much less than the potential for conceptualization. In contrast with Logan's model, however, the model within this thesis describes causal cognitive/behavioural sequences that explain how new forms could emerge, and the sequences related to language will be discussed shortly.

Many scholars have cited the capacity for symbolic conceptualization and communication as a key element in the origin of language (eg: Bickerton, 2003; Deacon, 1998; Marshack, 1976; Tomasello, 2003) and the positive role that humour played in the evolution of the hominin symbolic competence has already been discussed (see pp.137-141). Humour was a communicative/informatic system that involved symbolic attribution where gestures, vocalizations and objects could be associated with external referents, and as such, it stimulated the innovative disposition to learn massive numbers of symbols, which Hurford (2004) has claimed was the key step to the origin of language. In order for any type of language to emerge it was necessary to develop the coordinated integration of such symbols within a systemic whole, that could function in a domain-general telic capacity. As part of his minimalist program, Chomsky (2014) has asserted recursive merge to be of primary importance in the operation and origin of language and it has already been shown that the operation of humour involved a process of recursive merge (see pp.96-97). This is reminiscent of Corballis' proposal that "the modes of thought that made language possible were nonlinguistic, but were nonetheless possessed of recursive properties to which language adapted" (2014, p.xiii), but it will be shown that language would not have adapted to the precedent recursive system but emerged from it. The transition from humorous communication to linguistic communication would have involved

not only a substantial increase in operational complexity, but also the shift from autotelic to telic, and that type of process has already been outlined in relation to the emergence of analogical thought (see pp.118-121). It is proposed that an evolutionary path from autotelic to telic was essential for the emergence of language in order to explain the development of arbitrary constituent elements devoid of independent telic function and/or adaptive significance. As an autotelic system, the operation of humour also yielded mutual rewards for both expression and appreciation, and this is in agreement with Bickerton's assertion: "the first linguistic acts, whatever they were, must have been such that the speaker derived (at least) as much benefit from them as the hearer did" (2009 p.32). Bickerton uses the word "benefit" here, and the benefits of humorous behaviour have been discussed in some detail, but it is proposed that the word reward could easily be substituted to provide a plausible behavioural dynamic. So, it can be seen that the operation of humour involved communication and informatics within an autocatalytic, generative, hierarchical system involving recursive merge, but further consideration of specific functional aspects relating to cognition and related motor skills must be considered before constructing a more specific outline of how language may have emerged.

10.2 Laughter and speech

Laughter is a vocalization fundamentally connected with humour and thus, worthy of some consideration in relation to language. Laughter and speech may appear to be incompatible, because laughter "is not a linguistic construction but an acoustic one with no readily apparent semantic or syntactic features" (O'Donnell-Trujillo & Adams, 1983 p.175) and "to laugh is to momentarily lose control of speaking" (O'Donnell-Trujillo & Adams, 1983 p.187). In relation to the origin of language, these objections can, however, be easily addressed within the proposed model by considering humorous expressions as well as the laughter they stimulate. In terms of evolutionary background based strictly on biological considerations, there has already been a discussion on the development of physiology related to expression and perception of humour, and reference has been made to Provine's (2004) assertion that bipedalism facilitated the flexible breath control necessary for speech and laughing (see p.42). It is also possible that both smiling and laughter were evolutionarily important in communicative terms because they functioned as "tension release systems that have enabled and encouraged sustained face to face interaction" (Porteus, 1989 p.281).

Both speech and language are communicative vocalizations, and it has already been mentioned

that laughter is not a singular vocalization but has a degree of variety and complexity (for a review see Huber & Ruch, 2007), and that variations serve different communicative purposes (Coser, 1959). Based on research showing that laughter improved the performance of aphasics in language-based tasks, Potter and Goodman (1983) have speculated that humorous stimuli may serve to heighten right-hemispheric activity in the language relearning process. In addition, non-Duchenne laughter represents a voluntary vocalization that is frequently integrated with speech (Gervais & Wilson, 2005; Provine, 1993). In discussing the role of laughter in the emergence of language Caron states "(a)s hominids became humans, laughter would have become useful as part of an increasingly more abstract language, still able to express moods, yet now also capable of indicating a wish to initiate a playful mood or of commenting on the context" (2002 p.267). This position is supported by Szameitat et al: "diversification of human laughter in the course of evolution from an unequivocal play signal to laughter with distinct emotional contents subserving complex social functions." (2010, p.1264).

The communicative potential of laughter (and smiling) should not, however, be overstated. Owren and Bachorowski wrote that laughter is used primarily "to influence the affective states of listeners, thereby also affecting their behavior" (2003 p.183) and suggest a much lesser role for listener inferences. Laughter can to some degree, modify and contextualize the meaning of information and also serve an indexical purpose: "the placement of laughter, however, does matter. In this sense laughter is indexical; it is heard as referring to something, any hearers will seek out its referent"[147] (Jefferson et al., 1977 p.12), but as such, it remains a limited communicative tool. Despite its shortcomings hominin laughter would have helped to evolve the vocal and auditory faculties, and their related cognitive and behavioural processes to some degree. Non-Duchenne smiling and laughter would have been important because they involved voluntary control over facial muscles, the importance of which has been noted by Schmidt and Cohn: "Voluntary control over facial muscles, especially over the muscles of the mouth, is a hallmark of human nonverbal expression, and is likely due to the articulatory demands of human language" (2001 p.8). This represents an inversion of the evolutionary dynamics that have been proposed in this thesis, which assert that voluntary control of facial muscles did not evolve to meet the demands of language, rather, that voluntary control of facial muscles evolved to a

[147] This is also indicative of another dynamic that links humour with the capacity for symbolic expression.

point that allowed speech to emerge and the two co-evolved from that point onwards. Non-Duchenne laughter and smiling were two factors among the many (e.g. other vocalizations and facial expressions) that were involved in creating a proficiency in voluntarily manipulating a sufficient variety of musculature related to facial expressions and vocalizations to provide the requisites for the system of speech to emerge. What remains to be explored are the causal sequences by which this process may have occurred, and these will now be approached systematically within the framework of the five domains of language.

10.3 The five domains of language

Language is typically understood as comprising constituent elements that exist within the domains of phonology, morphology, syntax, semantics, and pragmatics (Gleason, 2005). From a functional perspective (as opposed to an evolutionary one), these domains are considered to be more or less hierarchical (Chomsky, 2005; Frank et al., 2012; Teh et al., 2006): morphemes are dependent upon phonemes; syntax is dependent upon phonemes etc. Consideration of humour's relationship with these five domains in an evolutionary context will help to determine whether or not the functional hierarchy is representative of a parallel hierarchical evolutionary progression.

10.3.1 Phonemes and morphemes

10.3.1.1 Vocal aspects

Phonemes and morphemes are necessarily hierarchically related as is indicated by Pinker's definition of a phoneme: "One of the units of sound that are strung together to form a morpheme, roughly corresponding to the letters of the alphabet" (2003, p.497). Essentially, phonemes are the fundamental single units of sound capable of being expressed by the human vocal apparatus and perceived by our auditory faculty, and morphemes are combinations of phonemes. In relation to the perception/cognition of phonemic elements in vocalizations, humour that involved (accidental or deliberate) vocalizations would have involved incongruity related to the intrinsic qualities of the vocalization, and/or patterns between multiple aspects within the vocalization, or between multiple vocalizations and/or contextually. In all these cases the cognitive cross-correlation of (phonemic) information would have occurred. Some of the qualities that could be cross-correlated would have been determined by the biological constraints relating to the perceived auditory information (e.g. pitch, volume, direction, timbre

etc.), while others would have been relative (e.g. duration, rhythm, situation). In the case of vocalizations voluntarily created to stimulate a humorous response, phonemes represented simple distinct vocal units and repeating, contrasting, and combining them would have had the potential to create humour. There is some ontological parallel to this in that these types of patterns are common in humorous parent/infant communication (Reddy, 2001; McGhee, 1979).

It is important to map out the relationship between humour and specific, cognitively abstracted phonemes/morphemes, because without them, language could not have emerged, and humorous communication would have been limited to holistic, non-particulated call signals and pantomime. Using distinct phonemes, repetition in combination with rhythm, volume, pitch etc. could be employed to create incongruities. This would have involved the creation of patterns within a specific vocalization, and these patterns could then be subsequently broken to produce humorous incongruity. Using multiple phonemes, humour could also be created with incongruities relating to the sequences involved. This would have provided exponentially greater numbers of potential variations, which made the use of multi-phonemic sequences a far more efficient method of producing humour. The basic dynamic of this shift was an upward spiral where higher levels of complexity in auditory vocal/auditory information yielded an increase in the potential for humour, so greater complexity would have yielded greater reward and benefit and thus such humour would have proliferated[148]. In concurrence with this, the capacity for analogical thought that humour engendered would have become involved and had the potential to imbue vocalizations with a telic aspect. At first, this may have related only to conative types of humour but gradually it would have transcended these.

In this scenario, any individuals with a greater capacity for vocal production would have been able to produce greater rewards and benefits. Such increased capacity for vocal production could have been the result of specific genetic factors such as the configuration of the forkhead box P2 (FOXP2) gene[149] which has been associated with speech and language (Lai et al.,

[148] This dynamic is illustrative of a broader dynamic stimulated by humour involving the random, non-telic (or telic) examination of the limits of human expression/perception/cognition within and across all domains. Humour related neophilia created a drive to explore novelty and the capacity for meta-cognition engendered by humour provided the cognitive /communicative raw material for such exploration.

[149] There has been some speculation that mutations of the FOXP2 gene in hominins played some role in relation to capabilities required for articulate speech, such as fine control of the larynx and mouth (Enard, 2011; Enard et al., 2002).

2001)[150], and the adaptive benefits of humorous behaviour would have ensured that such genetic characteristics were more likely to be passed on to succeeding generations. To put this in perspective, in a scenario without humorous interaction (and its related neophilia), a single individual capable of producing a greater variety of vocalizations would have no great adaptive advantage because their vocalizations could only serve as vocal signals if they were part of a shared social system, which would not be possible as they were the only ones capable of producing such sounds. Furthermore, such vocal signals would have been domain-specific and thus unlikely to be subject to any hierarchical progression. As such, the phenotypic anomaly would be of neutral or negative adaptive value. In a scenario with humorous interaction (and its related neophilia), these individuals would have possessed a valuable communicative skill that would have yielded rewards and benefits, including the enhanced likelihood of being selected as a mate, and such vocal signals were domain-general and potentially subject to further hierarchical progression.

The preceding passage describes an autocatalytic generative, hierarchical system by which the cross-correlation of categories of sound would have to have generated the ability to discriminate and voluntarily produce specific phonemes and morphemes. This dynamic can also be seen as constituting another manifestation within the suite of positive feedback loops that has already been discussed at several points in this thesis. A gradual process such as this would have to have been involved in order for vocalizations to evolve into the tidy packets of distinct phonemes and morphemes that appear in modern human speech. The ability to vocalize in this manner involves a coordinated system involving "intricate gestures of lips, velum, larynx, and tip, body, and root of the tongue" (Pinker & Jackendoff, 2005(a) p.208), which is unique to humans (Pinker & Jackendoff, 2005(a)). One of the roots for developing such ornate skills lies in the ability to first distinguish them within auditory input. This is an ability that the hominins in question would have had, as is witnessed in the fact that chimpanzees are able to detect a range of phonemic distinctions (Kojima et al, 1989; Kojima & Kiritani, 1989). Many primates, and particularly apes, have highly graded vocal repertoires utilizing phonemes, but they are not used as phonemes are in language, but are simply elements within holistic domain-specific calls (De Boer, 2005; Fedurek & Slocombe, 2011), so hominins would also have had the ability to

[150] It would be worthwhile to research the effects of laughter and smiling on epigenetics related to the FOXP2.

vocalize a range of phonemes. Phonemes were specifically identifiable aspects of auditory information that could be produced in vocalizations and therefore were communicative tools that could be used in creating perceptual incongruities in others i.e. humour. Hominins had the ability to perceptually and cognitively distinguish specific phonemes, so accidental phonemic incongruities that occurred as a result of vocalizations had the potential to be amusing. Biological and cognitive constraints dictate that vocalizations will tend towards certain patterns related to phonemic/morphemic combination and avoid others, (eg: tick-tock rather than tock-tick) (for a review see Pinker, 2003) so there were inherent phonemic patterns that were necessarily expected and such expectation could be broken and produce humorous incongruities. As such patterns did not have to be invented first in order for them to be broken because they were predicated by biology. Even the act of repetition, which is inherent in humorous expression, would have created patterns that could then be broken. There was plenty of phonemic "raw material" for the proposed model to function. Phonemic incongruities resulting in humour had the potential to be imitated, repeated, exaggerated and ritualized due to the drive from rewards, and the number of specific phonemes required for language to emerge was not large. Rotokas (a language from New Guinea) and Pirahã (a language from South-America) both have only 11 phonemes (Maddieson & Precoda, 1989).

This scenario provides a solution to a problem that has been inherent in origin of language studies: language has unquestionable adaptive value, but it has been much more difficult to determine the adaptive value of each of the constituent elements that were required in order for it to emerge (Bickerton, 2009). What, for example, was the adaptive value in developing the ability to articulate specific, distinct phonemes and morphemes without having the structure of language for them to function within or even any specific symbolic reference? The proposed model answers that question by presenting an autotelic scenario where there would have been a suite of rewards and benefits triggered by the ability to voluntarily create vocalizations with distinct phonemes and morphemes, thus creating a positive feedback loop which generated a cognitive/communicative system (and ultimately systems) of increasing hierarchical complexity. There is ontogenic support for this scenario in that similar patterns of phonemic/morphemic incongruity in vocal expressions can be seen in humour in early childhood development (Brousseau et al., 1996; Gleason & Ratner, 2005; McGhee, 1979; Yopp, 1995) that are concurrent with the development of language skills and positively correlated with language competence (Bryant et al., 1989).

10.3.1.2 Gestural aspects

As was mentioned earlier, it has been proposed by many scholars that gesture played an important role in the origin of language (e.g. Armstrong et al.,; Corballis, 1999, 2008; Petitto & Marentette, 1991). If gestures are narrowly defined as communication by means of hands, feet, or limbs it can be asserted that gestural communication is limited to humans and apes (Pollick & DeWaal, 2007). A review of this literature and the fundamental ideas that underlie this proposition is beyond the scope of this thesis and unnecessary because the problems with the gestural origin model are similar to those in gradual speech origin models, but it should be noted that because speech is universal, gestural origin theories necessarily assume a degree of integration occurred between the speech and gesture. Observations of such mixtures within expressions in childhood humour (e.g. Reddy, 2001; McGhee, 1980) support the notion that this type of integrative dynamic would have been present in hominin humour. Vocalizations would likely have typically occurred in conjunction with gestures, movements and facial expressions. While phonemes and morphemes are most often considered in relation to vocalizations they can also be considered as psychological units of linguistic structure (Stokoe Jr., 2005; Valli & Lucas, 2000), which is in agreement with the proposed notion that such singular elements would have been subject to cognitive abstraction. Seen this way, phonemes and morphemes constitute elements of sign languages as well as speech. It is reasonable to assume a possible role for facial expressions as well as gestures because facial expressions can communicate information (Ekman, 1993; Russell, 1994), are a component of gestural (Stokoe Jr., 2005) and spoken languages (Faisel & Luettin, 2003), and their use can be seen to have grammatical aspects (Jack et al., 2014; Reilly et al., 1990).

Ape gestures and call signal vocalizations both lack complex hierarchical structures and are transparent and iconic rather than opaque and arbitrary. In order for a hierarchical system to develop, there had to have been the cognitive cross-corollary of the constituent elements within a communicative social format. Gestural signals, like call signals, were, by themselves, evolutionary dead ends, as Bickerton points out: “(t)he ‘languages’ of ants and bees are evolutionary dead-ends; tens of millions of years later they haven’t developed into anything more ambitious, whereas language…is already a system of immense complexity and seemingly limitless productivity” (2009 p.141). Signals that serve a specific adaptive function tend to evolve only in relation to that function, as opposed to the scenario within the proposed model where domain-general, autotelically derived and evolved arbitrary elements functioned as integrative

pieces of an evolving hierarchical system. Used as tools to stimulate humorous response, the expression of arbitrary elements such as non-referential phonemes (in vocalizations or gestures) was autotelic; part of an informatic process that required no further immediate adaptive function. Humorous hominin behaviour would have produced amusement (including associated rewards and benefits) and the organization and sharing of information, and it would have led to the cognitive abstraction of discrete elements, which could be expressed vocally or gesturally, and these were necessary for the emergence of language.

10.3.2 Syntax

The preceding presents a scenario where there was the gradual development of integrative system involving vocalizations, gestures and facial expressions, and individual elements were identified, isolated and cognitively abstracted in order that they could be re-configured to create novel humorous expressions. This type of multi-modal communication is reminiscent of Porteus' statement: "the evolution of human language is largely a story about the establishment of capacities for mutual reference, a story involving a complex development of bodily gesture, facial expression and vocal intonation" (1989 p.284). The preceding description of the dynamics involving phonemic and morphemic constructions to produce humour shows that the process was syntactic[151] in nature in that it demonstrated rules and norms of combination dictated by the volitional creation of perceptual incongruity and or humorous recall. As such, it conformed to the following description of the syntactic process that exists in the language and music: "the mind converts a dynamic stream of sound into a system of discrete units that have hierarchical structure and rules or norms of combination" (Patel et al., 1998 p.717). The preceding quote was taken from a study that compared neural processing of syntactic incongruities in language and music and concluded that "language and music can be studied in parallel to address questions of neural specificity in cognitive processing" (Patel et al., 1998 p.717). The syntactic process decribed is also applicable to discerning humorous patterns in auditory input as well as musical or linguistic ones. The key concept is that of incongruities. In Patel et al.'s study, the identification of incongruities indicated the presence of syntactic structure: you can't have a break in a pattern without having a pattern to break. The cognitive/perceptual abilities and

[151] Syntax is taken to refer generally to the rules, principles, and processes involved in linguistic expressions.

constraints of hominins would have modulated their capability to detect patterns in sequences as well as in the constituent elements within singular vocalizations. Humour would have provided a behavioural framework for the voluntary manipulation and appreciation of such patterns, thus yielding benefits and rewards. There would have been "normal" (i.e. congruous) patterns and "funny" (i.e. incongruous) patterns, which could be discovered by accident (or created), then imitated and ritualized. This ritualization would in turn create further normative patterns which could then be broken in the continuation of a hierarchical process.

As was stated, this process would have been predicated on numerous cognitive and/or biological factors as well as, or in combination with, ecological ones. For example, there is a cognitive mechanism that spontaneously encodes positional information of sounds within sequences from auditory temporal sequences in chimpanzees as well as humans (Endress et al., 2010) and it has been proposed that this was recruited by language to "constrain the form that certain grammatical regularities take" (Endress et al., 2010 p.483). There has been some scholarly consideration of such relevant constraints (for reviews see Fitch, 2000; Lieberman et al., 1992), and Pinker and Jackendoff note "certain animals can make auditory distinctions based on formant frequency, that tamarin monkeys can learn to discriminate the gross rhythms of different languages, and that monkeys can perceive formants in their own species' vocalizations" (2005 p.206). Essentially, it would have been possible for hominins to detect patterns in expressions, and any expressions that incorporated distinguishable patterns would have had the potential to yield perceived incongruities and thus, humour. In auditory terms such patterns relate not only to the relations between the intrinsic qualities of the sounds involved, but also their contextualization. The capacity for this type of processing has been described in the notion of Auditory Scene Analysis[152] (Bregman, 1994), which also ascribes a semantic aspect.

In the proposed model, the manipulation and reconfiguration of humorous expressions would have created a shared body of hierarchically evolving syntactic structures, and the suite of associated positive feedback loops gave this process an autocatalytic, generative quality. In this way hominins would have developed the capacity to identify, and perceptually and cognitively

[152] "Auditory scene analysis (ASA) is the process by which the auditory system separates the individual sounds in natural-world situations" (Bregman, 2008 p.861).

abstract and parse, distinguishable patterns in gestures, facial expressions, and vocalizations and thus create a shared body of information that could be applied in future communication. As such, there is a direct correlation of this dynamic and Deacon's description of the development of a symbolic system (ie: language) "The rules of combination that are implicit in this structure are discovered as novel combinations are progressively sampled" (1997, p.100).

In terms of the viability of such a scenario in cognitive terms, it has been shown that neural processing of syntactical information is not dependent on language (Lau et al., 2008; Wilson-Mendenhall et al., 2013), which supports the idea of simple syntax emerging in hominin communication before the emergence of language, and further support can be seen in Knight's paper "Play as Precursor of Phonology and Syntax" (2000) which states

> (s)uppose certain internal variations within a primate vocal sequence reflect intentional manipulation expressed only as 'idle play'. Provided no risks are entailed, conspecifics might respond with relaxed 'play' vocalisations of their own. If such call-and-response exchanges served bondng functions, sophisticated capacities for detecting and producing signal variety might evolve (2000 p.1)

Knight's model differs from what is proposed in this thesis in that it assumes a musical element and only briefly refers to humour, but it does refer to the importance of humour as a "leveling device among early hunter-gatherers…helping to sustain distinctively human levels of in-group trust and mutuality on which speech in turn depends" (2000 p.1). Knight's model also has significant parallels with aspects of the model proposed in this thesis, as is illustrated by the following passage: "Incipiently language-like properties of both vocal and whole-body play…would now characterize in-group communication, with recently evolved mimetic skills yielding a system more complex and syntactical than anything known before" (2000 p.1).

Within the proposed model, it is humour, rather than broader activity of play, that would have played the critical role, though there is significant overlap between humour and play as was discussed earlier (see pp.54-55). Within this scenario, the increased complexity in cognitive, psychological, behavioural, and ecological domains caused by general humorous behaviour, along with associated neophilia, would have produced an increasing variety of combinations in gestures, expressions, and vocalizations that would have been expressed subject to the emerging/evolving set of syntactic rules. This growing number of gestures, expressions, and

vocalizations would have provided the raw material for language, or what Bickerton refers to as a "sizable vocabulary whose units could be organized into complex structures" (1995 p.51). Syntax can be seen to have emerged as a hierarchical product resulting from the informatic processes involved in the operation of humour and the analogical thought it engendered. This scenario is similar to that proposed by Donald, which is well described by Knight et al.:

> Donald finds evidence for a prelinguistic mode of communication in the gestures, facial expressions, pantomimes and inarticulate vocalisations to which modern humans may have recourse when deprived of speech. 'Mimesis' is Donald's term for this analog, largely iconic, mode of communication and thought. The mode requires a conscious, intentional control of emotionally expressive behaviours, including vocalisation, that is beyond the capacity of other primates (2000 p.9).

10.3.3 Semantics

The preceding offers a causal model for the hierarchical evolution of phonology and syntax but it begs for answers regarding the issue of meaning: if humour is assumed to have been created by breaks in perceptual/cognitive patterns dictated by perceptual/cognitive constraints and ecological norms but devoid of any external referents (i.e. without any symbolic meaning), wouldn't it have simply resulted in the production of patterns within strings of phonemes/morphemes with a simple syntactic structure similar to "baby-talk"? This would not have been the case, however, due to humour's use of iconic and indexical expressions (see pp.137-141), and the incorporation of context through displacement. Many animal call systems are considered to have semantic aspects (eg: Boero, 1992; Seyfarth et al., 1980; Zuberbuhler, 2000), which suggests that hominin signals would have had them as well. A specific example of such semantic content may have existed in relation to phonemic/morphemic expressions and variations used to identify and differentiate objects and/or individuals, thus incorporating symbolic attribution. For example, if an individual was strongly associated with a specific vocalization or gesture, the sound could be used as a symbolic means of identifying that individual. As such, the imitation of a single expression associated with an individual could have served to reference that individual regardless of whether or not they were present. In a humorous context, such expressions used to identify a referent would have been simplified and exaggerated as per comic dynamics. If these expressions stimulated a humorous response, they had the potential to be repeated, which would have entrenched the association in social

memory and created an abstracted conception that could be employed in subsequent communication. In short, that person or object would have been given a name. It should be noted that within the proposed model, the emergence of such names (and other iconic/indexical expressions) did not result from practical (i.e. telic) considerations, but was predicated on autotelic dynamics, which may have subsequently evolved telic functions. In a pre-linguistic scenario humorous expression (and/or music) would have been the primary source of autotelic vocalizations and as such, would have served as a source from which to derive names, which could then be used in a telic fashion as referential tools. Names, of course, lack the arbitrariness of language, but it would have been possible to modify a name using a descriptive phoneme, based upon biological constraints. One example of this is "the association of high acoustic frequency with smallness and low acoustic frequency with largeness" (Ohala et al., 1997 p.5) that is reflected in the linguistic structures of related words across cultures (Ohala et al., 1997). Phonemes/morphemes with such acoustic qualities could have been used as descriptive modifiers for iconic/indexical vocalizations involving displacement, and these would qualify as having been linguistic expressions. This type of thing may have occurred accidentally at first, but such expressions would have been repeated, imitated, ritualized and enculturated as per the process described at several points in this thesis.

So it can be seen that call systems would have incorporated sematic content, which could then have been utilized within humorous expressions. As such, the domain-general nature of humour in combination with the cross-correlation of information between multiple schemata was able to take units of semantic communication previously confined to specific domains, and cognitively create abstract conceptions of them, which could then be applied in subsequent communication. Furthermore, specific calls could also be cognitively processed in relation to their constituent phonemic/morphemic elements, which could potentially be reconfigured to create humour, then ritualized and evolved into domain-general telic expressions. Use of this type of semantic content would have involved syntactical constructions that were "lexical" rather than strictly "phonological", in that they functioned as "rule-governed assembly and reassembly not just of phonetic representations but of semantic ones" (Knight, 2000 p.1) with digital, rather than analog, distinctions between meanings.

Existing call signals (gestures, facial expressions and vocalizations), would have been likely to occur in hominin humorous expressions for a number of reasons. Firstly, the communicative repertoire of hominins was necessarily more limited in a pre-linguistic context: there were only

so many ways to express things so they would have to have used the tools at their disposal. Existing call signals were also likely to be used in humour because of their high degree of salience (i.e. they were noticeable and important in the repertoire of hominin communication), and higher levels of salience have also been positively correlated with the successful creation of humour (Goldstein et al., 1972). Calls from existing hominin call systems would also have tended to have emotional associations and, in this way, they would have had the potential to stimulate emotional arousal. This would have facilitated humorous behaviour because, as has already been asserted, moderate levels of arousal are conducive to humour (Apter & Smith, 1977; Berlyne, 2014; Rothbart, 1977). Finally, and perhaps most importantly, the use of established telic expressions outside of their typical context (i.e. displaced) would have created incongruity in itself, and would thus have made such expressions fundamentally humorous. For example, within a situation involving positive emotional valence, making an expression signaling the presence of an animal when there was no animal present, or while indicating an inanimate object, would have been incongruous, and thus, potentially amusing. Bearing in mind the preceding it can be seen that expressions (facial expressions, gestures, and vocalizations) with specific iconic and/or indexical meaning (i.e. with semantic content) would likely have been used in scenarios displaced from their original context, which would have constituted a further advance in hominin symbolic competence, and this would have occurred in a shared communicative context.

Returning to the broader question of how pre-linguistic humour would have involved/fostered semantic aspects, it can be seen that the use of iconic and indexical expressions, and the incorporation of displaced call signals introduced logical, semantic aspects into humorous communication. Pre-linguistic humour would not have been amusing babble; it would have involved the communication of specific information in a hierarchically evolving symbolic manner. This picture runs contrary to the traditional logic that has been applied to the subject of language origins in a social/behavioural frame, which tends to ask for what adaptive reason did hominins need language? and/or what adaptively significant behaviour might have been conducive to the emergence of language? (e.g. Bickerton, 2016; Pinker, 2003). Such approaches will tend to be dead-ends because they can only explain domain-specific call systems built on holistic expressions. It required a domain-general autotelic system for the discrete elements of language to be identified, cognitively abstracted and cross-correlated across schemata, and then intentionally reconstructed and expressed in novel forms imbued with symbolic meaning and the potential for future telic application. Once this type of system

was operational, further evolution of semantic content could have occurred because of the possibility of humour based specifically on semantic incongruities, i.e. expressions that were not predicated on incongruity of their intrinsic qualities, but on incongruities derived from symbolic meaning. Once again, such expressions may have first occurred by accident and then been subsequently repeated, but regardless of whether it began deliberately or accidentally, it constituted the creation of humour through incongruity of meaning: it was semantically predicated humour that would have stimulated the capacity for lexical semantics.

The proposed model is applicable to both vocal and gestural language origin scenarios, but it is suggested that a multi-modal scenario is the most likely evolutionary candidate. Multi-modal humorous expressions can also be seen to have facilitated the emergence of the semantic element as suggested by Arbib et al.: "gesture and then pantomime offered a path to an open semantics" (2008 p.1053). Facial expressions should also be included as contributing factors. The potential for this is well illustrated by the following passage by Paul Bouissac taken from his book "The Semiotics of Clowning":

> (t)he face packs into its relatively small surface many other biological functions, such as breathing, smelling, hearing, seeing, eating and drinking, and eliminating mucus and other secretions. All these biological imperatives, including the communicative ones, are bound to constrain each other and create inferences (2015, p.22).

In sum, hominins would have been capable of semantic communication and humour served as a mechanism that allowed the voluntary creation of expressions with meaning, with or without the use of existing domain-specific calls with symbolic significance. Furthermore, humour would have involved the voluntary cross-correlation of related information across multiple schemata, as well as the cognitive abstraction of holistic expressions and their constituent elements. As such, it did not only facilitate symbolic/semantic expression, it caused the total body of hominin symbolic/semantic expressions to become part of an coordinated integrated system of communication that hierarchically evolved through the suite of positive feedback loops that has been discussed.

10.3.4 Pragmatics

Several scholars have noted the relationship between humour and pragmatics (eg: Attardo, 2003; Curco, 1995; Yus, 2003). In discussing this connection, Yus draws on Sperber and Wilson's Relevance Theory, and has proposed "a single cognitive principle of relevance applicable to the interpretation of all types of discourse, humorous discourses included" (2003 p.1327). He attributes this to "a (biologically rooted) human tendency to try and find relevant information in the utterances and non-verbal behavior that people use in order to communicate" (2003 p.1327). In neurological terms, it can be seen that impairment of the ability to process relevance (which is centred in the amygdala[153]) is a contributing factor to autism (Zalla & Sperduti, 2013)[154], which in turn is negatively correlated with the capacity for humour. The biologically rooted aspect that Yus refers to is more general and can be associated with the notion of salience, (which was mentioned earlier in regard to semantics) and the two terms are often used interchangeably in neurophysiological studies (eg: Bisley & Goldberg, 2003; Robinson & Petersen, 1992; Thompson & Bichot, 2005). Fecteau and Munoz distinguish the two, defining salience as "the physical, bottom-up distinctiveness of an object. It is a relative property that depends on the relationship of one object with respect to other objects in the scene" (2006 p.382), while "the relevance of an object influences how it is processed in oculomotor structures and elsewhere" (2006 p 387). Essentially, salience relates to perceptible/definable qualities (gestalt) and semantic aspects relating to the meaning of such qualities, while relevance relates to the building blocks of contextual interpretation and results in pragmatics. In terms of humour, perceived incongruities relating to both salience and relevance have the potential to yield humour.

Bearing in mind the preceding, it can be seen that the cognitive/perceptual mechanisms underlying pragmatics are ancient and exist in many animals as part of their decision making processes. Typically such processes are rapid but less accurate when affectively mediated and slower but more accurate when cognitively mediated (Chittka et al., 2009) and they allow

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[153] It has also been shown that the amygdala is involved in humour processing due to its role in the resolution of incongruity (Nakamura et al., 2017).

[154] The notion that autism spectrum disorders (ASD's) involve impairment related to relevance conflicts with the standard assumption that ASD's only involve impairments in socially related cognition. The proposed model can be seen to show a bridge between the two by illustrating how social cognition evolved from broader cognitive foundations and functionally integrated information derived from these foundations.

animals to determine levels of relevance in cognitive/perceptual information, helping to determine the resulting behaviour. In relation to the human cognitive capacity for determining relevance Van der Henst and Sperber state:

> …because of the way their cognitive system has evolved, humans have an automatic tendency to maximize relevance. As a result of constant selection pressure towards efficiency, perceptual mechanisms tend automatically to pick out potentially relevant stimuli, memory mechanisms tend automatically to store and, when appropriate, retrieve potentially relevant pieces of knowledge, and inferential mechanisms tend spontaneously to process these inputs in the most productive way (2004 p.232).

While this statement clearly frames the faculty of cognitive relevance, it fails to address why it should be unique to humans and how this faculty may have evolved? The evolutionary model presented in this thesis addresses both these issues. The 8 stages outlined in the emergence of humour (pp.74-107) suggest that a limited capacity for cognitive relevance would have been sufficient for the processing of simple forms of humour. Humorous behaviour then introduced a reward-driven communicative/informatic system predicated on the perception/cognition of incongruities, which over time enhanced the hominin ability to cognitively process relevance. This would have involved the cross-correlation of related pragmatic information across schemata, and the creation and sharing of novel, integrated expressions imbued with pragmatic significance**.** The development of Theory of Mind engendered by humour also would have played a significant role in the development of pragmatic aspects of communication. The existing capacity for of an individual to cognitively process relevance would have directly mediated the level of success or failure of humorous expressions: greater shared relevance would have yielded greater reward. This would have created a dynamic wherein humour and the capacity for both cognitive relevance and communicative relevance would have co-evolved in a type of upward spiral, contributing another aspect to the suite of hierarchical positive feedback loops that has been described.

Within the proposed model it can be seen that pragmatics evolved as part of a combined cognitive/informatic and communicative processes. In concurrence with this, the faculties of analogical thought and causal reasoning engendered by humour would have facilitated the development of the hominin perceptual/cognitive capacity to become consciously aware of the pragmatic implications of semantic expressions, thus leading to the conscious manipulation of

pragmatic dynamics in expressions for humorous reasons (i.e. conative humour) and eventually, for practical, telic reasons as well. As such, humorous behaviour promoted the evolution of pragmatics in both cognition and expression long before there was any conscious manipulation of pragmatic dynamics to create humour. Essentially, humour's central aspect, the perception of incongruity, could be applied directly to unconsciously held pragmatic information, which could then be cognitively abstracted, and then incorporated into expressions that would then be held in a shared body of social knowledge.

10.3.5 Summary

Pre-linguistic hominins would have created humour through the cognitive processing and expression of incongruity relating to information derived from all five primary domains of language. As such, humour served as a mechanism by which such information was abstracted, shared, hierarchically evolved, and integrated, which constituted a communicative/cognitive co-evolutionary dynamic. The functional hierarchy of the five domains of language does not represent a parallel for the path of evolutionary progression that occurred, instead language can be seen as the product of a coordinated integration of these five domains in a communicative format. Pre-linguistic humour would have involved the use of phonemes, morphemes, syntax, semantics and pragmatics, and together with the capacities for analogical thought and causal reasoning that humour engendered, there was a gradual integration of these aspects into a coordinated hierarchical system, which resulted in the emergence of language. In this way, the telic system of language can be seen to have been derived from the autotelic system of humour.

The five domains of language can be roughly divided into three separately developing systems that were gradually integrated: i) phonemes, morphemes and syntax ii) semantics and iii) pragmatics. Phonemes, morphemes and syntax co-evolved in vocalizations, gestures and facial expressions. Semantics evolved due to the use of iconic and indexical expressions, perceptual/cognitive constraints, and the incorporation of existing call signals (vocalizations, gestures, and facial expressions). Displacement played a key role in the evolution of semantics in that displaced expressions were both fundamentally humorous as well as critical in developing the ability to communicate information abstracted from previously existing telic domain-specific call systems. Information based on pragmatics, relevance and salience can be seen to have been source information for the processing of incongruity and thus, the creation of humour. It is proposed that humorous behaviour stimulated the evolution of these three systems

and also provided a mechanism by which they could be integrated and unified in a communicative format.

As has been mentioned, the proposed model contributes a significant constribution to knowledge by providing a solution to one of the recurring issues in origin of language research: how and why would the development of arbitrary elements required to create language have occurred without any identifiable adaptive function(s) for their expression in a pre-linguistic context? (e.g. Bickerton, 2009). While call systems had adaptive functions, the development of phonemic/morphemic constructions that conformed to syntactic rules was not a requirement for such expressions, so what why would it have evolved? Hurford addresses this issue in relation to spandrels:

> Lightfoot's (1991) position is that the formally interesting features of the language faculty, which give human languages their characteristic features,… are not particularly fitness-enhancing; the human language capacity is more complex than it needs to be, and even in places dysfunctionally complex. Such features as Subjacency may indeed be, Lightfoot argues, just accidents (spandrels); but scientific methodology abhors accidents, and a powerful theory predicting the occurrence of such features would be preferable, if one could be found (1999 p.180).

The model within this thesis offers just such a theory (though specifically tackling the issue of the origin of subjacency is beyond the scope of this thesis). The proposed model shows an evolutionary progression that fulfills Hurford's criteria and incorporates Deacon's related notion that relaxed selection played a role in the emergence of language (2010). Within the model, phonemes and morphemes were like toys that served to amuse, or to stretch the analogy further, like game pieces in the "game" of humorous interaction; a game that conformed to simple syntactic rules, some of them biologically rooted. This game served as a system for hominins to explore/share their cognitive limitations and resulted in a diversity of shared thoughts/ideas. As such, the isolation, abstraction, combination, and manipulation of phonemic/morphemic combinations evolved in a manner that allowed:

1) the emergence of shared novel symbolic vocalizations utilizing specific combinations of phonemes/morphemes intended to communicate specific information;
2) the use of combinations of such vocalizations and;

3) the co-opting and modification of existing telic vocalizations through displacement.

Pre-linguistic humour would have involved the syntactically based expression of configurations of arbitrary, symbolic expressions, which is very similar to modern-day non-verbal clowning. In this way, the emergence of language did not follow a linear path where call-signals and/or gestures morphed into language. Instead the dynamic was a tri-partite one that involved a) the autotelic informatic cognitive/perceptual processing and communication of discrete arbitrary elements and forms, b) the incorporation, abstraction, and reconfiguration of existing communicative vocalizations/gestures/facial expressions in a displaced autotelic format and c) the incorporation of pragmatic elements evolved (in part) due to cross-comparative cognitive operations involved in the processing of humour. Essentially, expressions had to be particulated, abstracted and parsed in order for a hierarchical system incorporating arbitrarity to be created, and this was only possible in a domain-general autotelic format that rewarded and benefited behaviour involving the cognitive cross-comparison of information across schemata. It is also worth repeating that the importance of the autotelic dynamic in an evolutionary context is supported by Sperber who asserted that the human cognitive/communicative capacity for relevance is partly the result of “a uniquely massive investment in cognition with the systematic gathering of information beyond not just immediate practical usefulness but also without any definite future usefulness” (2017, personal correspondence e-mail).

10.4 Chomskyian model

While the preceding presents a moderately comprehensive argument for the role of humour in the emergence of language, it is still necessary to consider the proposed model in relation to other origin of language theories in order to address relevant questions and issues. Rather than review a comprehensive list of the sum of evolutionary requirements for the emergence of language put forward by the sum of origin of language theories, it is more practical to simply consider evolutionary requirements within a single proposed framework and add additional information if and when it is necessary. The frame that will be used is that proposed by Hauser, Chomsky and Fitch in their paper “The faculty of language: what is it, who has it, and how did it evolve?” (Hauser et al., 2002) because it is an acknowledged paper, which encapsulated and evolved Chomskian ideas in a framework that cited biological and behavioural aspects.

Chomsky (1986) has proposed that the faculty of language is innate in humans and that its universal features constitute a universal grammar. Previous to the 2002 paper he tended to avoid theorising regarding possible evolutionary mechanics of how such may have evolved, but the 2002 paper resolved this, taking into account a range of neurological, biological, and phylogenic perspectives[155].

The 2002 paper states

> …a distinction should be made between the faculty of language in the broad sense (FLB) and in the narrow sense (FLN). FLB includes a sensory-motor system, a conceptual-intentional system, and the computational mechanisms for recursion, providing the capacity to generate an infinite range of expressions from a finite set of elements. We hypothesize that FLN only includes recursion and is the only uniquely human component of the faculty of language (2002 p.1569).

Put simply, the paper proposes that language must be considered in terms of the sensory-motor system, the conceptual-intentional system, and the computational mechanisms for recursion, with particular emphasis on recursion. The term "computational mechanisms" is reflective of Chomsky's assertion that language should be seen as computational system rather than a communication system (Chomsky, 1986). This position is summed up well by Knight et al. as "the belief (shared with many other linguists, e.g. Bickerton 1990 and Jackendoff 1994) that language is not so much a system of communication, on which social selection pressures might indeed have come to bear, as it is a system for mental representation and thought" (2000 p.3). The counter-argument that language is primarily a communication system (as opposed to a computational one) is one that is supported by many academics (eg: Newmeyer, 1991; Pinker & Bloom, 1994). Within the proposed model, language can be seen as having been derived from a system involving the co-evolution of cognitive and communicative elements. Pre-linguistic humour would have functioned as both a system of communication, and a system of mental representation and thought, which is reminiscent of Logan's definition of language (language = communication + informatics) (1995, 2000), that was covered earlier (see pp.206-207).

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[155] This paper stimulated some debate, most particularly demonstrated in Pinker and Jackendoff (2005, 2005(b)) and Fitch et al., (2005).

I will now discuss the sensory-motor system, the conceptual-intentional system, and the computational mechanisms for recursion. This will be done in relation to both accidental and voluntary humour in order to present a clear picture based on causal sequences within an evolutionary progression. The following section serves primarily to review material already discussed within this thesis and to place it in context and contrast with the Chomskeyan model of the origin of language.

10.4.1 Accidental humour

It is logical that the earliest forms of hominin humour would have been accidental in nature: perception is necessarily a more cognitively simplistic operation than perception and voluntary creation. Accidental humour involved the perception/cognition of incongruities and cross-correlation of input information with the existing body of humorous memories/associations and as well as all resulting laughter and smiling responses.

i) Accidental humour in relation to the sensory-motor system

The sensory-motor system would have been involved in the audio/visual perception of externalities related to incongruity, in the production of smiling and/or laughter responses, and in the subsequent perception of these responses and possible production of further "contagious" smiling and/or laughter. As such, the increased production and perception of smiling and laughter, in conjunction with associated rewards and benefits, would have resulted in the enhancement of related sensory-motor aspects (eg: facial muscles, larynx) and possibly have had an impact on gene expression (see p.174). These, however, would seem to have been relatively minor effects and there would have been a great deal of continuity in relation with previously existing dynamics relating to sensory motor (i.e. biological) aspects. The perception of external incongruities was biologically rooted as a necessary part of the survival instinct (i.e. differences represented potential danger) and as such, this early phase reflected a novel functioning of previously existing sensory-motor capabilities rather than any type of profound and/or saltational progression. This continuity in biological systems is an important aspect of the proposed model and shows it to be in agreement with the gradualist approach of Pinker and Bloom (1994), Deacon (1998) and others (eg: Dediu & Levinson, 2013; Donald, 1991).

This is not to say that there were no significant, language relevant, sensory-motor systems advancements being made during the same period separate from humour (eg: related to vocal call systems, tool making etc.), but at this stage, humour played little to no role in such dynamics. There was one sensory-motor aspect that was related to laughter that was also separate from the operation of accidental humour, which was the presence and use of the risorius muscle. The risorius muscle is required for non-Duchenne (i.e. voluntary) smiling and laughter and exists in humans and higher apes, so it is reasonable to believe it has been present in all hominins. The use and enhancement of sensory-motor aspects related to the production and perception of voluntary smiling and laughter would also have constituted an advance in hominin communication-related sensory motor systems.

ii) Accidental humour in relation to the conceptual-intentional system

Hauser, Chomsky and Fitch (2002) refer to the following as representing the conceptual-intentional system: Theory of Mind; the capacity to acquire non-linguistic conceptual representations, use of referential vocal signals, the use of rational, intentional imitation; and voluntary control over signal production as evidence of intentional communication. Their analysis of these capacities in other primates indicates that, with the exception of Theory of Mind, the foundations of the human conceptual-intentional system are present in non-human primates, and Pinker and Jackendoff (2004) are largely in agreement with this position. In the "accidental" stage, humour would have lacked both the use of rational, intentional imitation, and voluntary control over signal production: it was not a voluntary/intentional process. The cognitive processing of a humorous event was, however, centred on the acquisition of a non-linguistic cognitive concept representation. The event itself was perceived, but the attribution of amusement created a cross-correlated conception and thus represented a progression from percept to concept. Laughter and/or smiling served as referential vocal signals (albeit involuntary ones) denoting the sharing of such conceptions, and they created rewards/benefits within a process involving the communication of one individual's mental state to another. As such, humour served as a mechanism that enhanced the capacity for Theory of Mind, as was discussed (see pp.85-86). The capacity for Theory of Mind would also have been enhanced by the amount of face-to-face contact and joint attention (see pp.88-89) that was potentially involved in accidental humour. In addition to this, accidental humour would have served as a catalyst for antiphonal laughter stimulating improvement in social memory and perceptual sensitivity to the actions of others. This, in turn would have increased levels of success in

subsequent joint-action tasks, and it is possible to view the development of language as just such a task.

One aspect of the conceptual-intentional system that was not touched on in either the Hauser et al. or Pinker and Jackendoff papers was the capacity for analogical thought and/or causal reasoning. The manner in which humour facilitated these capacities in hominins was outlined earlier (see pp.118-121), but to recap, it was proposed that humorous recall (see pp.35-38) and the cognitive processing of degrees of difference (i.e. incongruities) in a situation of positive emotional valence, stimulated the faculty to distinguish degrees of sameness in a manner reminiscent of Gestalt notions of foreground/background. In the accidental phase, this was not manifested in any type of expression, but the cognitive capacity was, nonetheless, being enhanced in a process that yielded rewards and benefits. In this scenario, analogical thought would have preceded and to some degree predicated, the structuring of language[156]. This would be in agreement with Hofstadter's (2001, 2013) notion that analogy lies at the core of human cognition and Lakoff's & Johnson's (2008) notion that metaphors (a type of analogy) lie behind virtually all linguistic expression. Fauconnier and Turner provide a good, brief summary of the relationship between analogical thought and language: "(a)nalogical mapping, traditionally studied in connection with reasoning, shows up at all levels of grammar and meaning construction, such as the interpretation of counterfactuals and hypotheticals, category formation, and of course metaphor, whether creative or conventional" (1998 p.135).

As such, humour's role in the emergence of analogical thought was important in the evolution of hominin conceptual-intentional capacities relevant to the emergence of language. This added a hominin capacity relevant to the emergence of language that, much like Theory of Mind, is seen only in a rudimentary state in non-human apes (Gillan et al., 1981; Hollyoak et al., 2001).

iii) Accidental humour in relation to computational mechanisms for recursion

[156] The progression was roughly: particulation / abstraction /conceptualization of perceptual input in accidental humour followed by the ability to manipulate and express such information in voluntary humour…language represented a more complex telic form that gradually emerged from this process.

Turning now to computational mechanisms for recursion in accidental humour, it is first necessary to provide a more detailed definition of what Hauser et al. are referring to when they apply this term. In order to understand this it is necessary to return to the notion of merge (see pp.96-97), which Chomsky defined as “an indispensable operation of a recursive system ... which takes two syntactic objects A and B and forms the new object G={A,B}" (Chomsky, 1999 p.2). At the accidental phase, humour did not involve syntactic objects, but it did involve a rudimentary recursive system involving mental conceptions where the perception of an event was cross-correlated with expectation based on memory, which produced a novel humorous conception.

Humour did not miraculously introduce the process of recursion, rather, it involved a cognitive manifestation of a general principle known as the particulate principle of self-diversifying systems which is described in the following way by Studdart-Kennedy and Goldstein:

> According to the particulate principle, the only route to unbounded diversity of form and function is through a combinatorial hierarchy in which discrete elements, drawn from a finite set, are repeatedly permuted and combined to yield larger units higher in the hierarchy and more diverse in structure and function than their constituents. The particulate units in physical chemistry include atoms, ions, and molecules, in biological inheritance, chemical radicals, genes and proteins, in language, gestures (as will be argued below), segments, syllables, words and phrases (2003 p.2).

The capacity for recursive processing has been noted in relation to visual information (Pinker & Jackendoff, 2005(a)), music (Jackendoff, 2009; Kinsella, 2010), and Theory of Mind: “theory of mind provides perhaps the most uncontroversial example of non-linguistic recursion: I can embed the thoughts and knowledge of others within my own leading to recursively embedded conceptual structures” (Kinsella, 2010 p.182). In the case of accidental humour this can be rephrased to I can embed thoughts and knowledge generated through the cross-correlation of perceptual and cognitive information across schemata within my own leading to recursively embedded abstract conceptual structures. In this case, the “particulates” involved are the specific identifiable features/qualities of that which is perceived as per Gestalt psychology or Feature Integration Theory (see pp.21-22).

While accidental humour had recursive aspects, it fell far short of providing a system appropriate for the creation of language (i.e. creating an infinite number of expressions from a

finite set of elements) but it did represent an important cognitive step. This simple process of recursion was theoretically infinite in that there were an infinite number of possible ways incongruity could occur in perceptual input and an infinite number of ways this input could be cross-correlated to produce novel conceptions, but there was no voluntary expression; it was not a creative process. The specifics of the computational operation were not directly communicated and in this way the proposed model could possibly be construed as being in agreement with Chomsky's notion of computational origins, but when considered in ecological context it can be seen that such computations were socially and situationally predicated, and as such, cannot be considered in isolation from the broader notion of communication. The presence of simplistic recursion in the earliest forms of humour can be seen to demonstrate one of a series of gradual steps that eventually produced the hominin capacity for language. This runs contrary to the Chomskyan notion of a saltational or "hopeful monster" explanation[157] (i.e. that some specific, cognitively based, genetic mutation triggered the functioning of the faculty for language). The proposed model provides a gradualist solution to the problem of determining the origin of a hominin computational system involving recursive merge. Rather than presenting a theory wherein language appeared fully formed, it can be seen that it is possible to define a specific intermediate stage (or stages) where a recursive cognitive system was operating, and this system was self-perpetuating due to the rewards and benefits it yielded.

The importance of rewards (and benefits) has been consistently stressed throughout this thesis, but specific consideration of the role of rewards is merited in relation to the topic under consideration. When attempts have been made to teach language to higher apes, researchers have had to provide extrinsic rewards in order to effect the necessary motivation. This is typically done with food (e.g. Rumbaugh, 2014; Tomasello et al., 1997), but tickling has also been used as a reward and shown to be effective in helping to stimulate learning of gestures, combinations of gestures etc. (Fouts et al., 1976; Gardner & Gardner, 1969; Premack, 1971). Gardner and Gardner stated "tickling is the most effective reward that we have used with Washoe" (1969 p.669) and they also used smiling and frowning to signal approval and disapproval (Gardner & Gardner, 1989). The use of tickling as a reward differs from typical food

[157] In theory, if the capacity for humour can be found to be specifically genetically determined, then humour itself might be seen to have a saltational origin, though it is asserted that the gradualist picture that has been presented for humour precludes the need for such.

based operant conditioning, and its efficacy in relation to language learning in apes may be due in part to dynamics relating to affect and arousal (for a review see Hixson, 1998). Skinner's view that traditional operant conditioning stimulates language acquisition (in ontogenic terms) has long been discredited (e.g. Chomsky, 1988), but in the proposed model, the reward is an intrinsic, endogenous, affective one, so the dynamic is more like that described by Rolls as stimulus-reinforcer association learning (2013). It is notable that tickling serves as an effective reward in language learning, and that humorous behaviour provides similar rewards substituting the physical cause and effect stimulus of tickling with a process involving informatic, cognitive processing as stimulus. In functional terms the operation of accidental humour put the hominins in question in a position where a hierarchical positive feedback loop stimulated the exponential development of associated aspects (computational, conceptual/intentional and sensory-motor) that were constituent in the emergence of language. Also, as was stated earlier, the motivational component of endogenous reward was essential in order for any type of initially autotelically derived faculties (i.e. the ability to create meaning using combinations of arbitrary symbols) to emerge.

10.4.2 Voluntary humour

In general terms, voluntary humour had several aspects in common with language: its mechanism was innate, and its functional constituents were variant, learned throughout the individual's life, and comprised a hierarchy. The category of voluntary humour is intended to encapsulate the entirety of all the stages following accidental humour that preceded the emergence of language. It is not assumed to necessarily include ramifications associated with the emergence of the aesthetic faculty, though it may be reasonable to make such an assumption.

i) Voluntary humour in relation to the sensory-motor system

In sensory-motor terms, voluntary humour would have involved the physical expression and

perception of humour, as well as resulting laughter/smiling responses[158]. The dynamics related to communicative vocalizations, gestures and facial expressions caused by pre-linguistic humorous behaviour would have stimulated evolutionary modifications (via sexual selection, epigenetics, the Baldwin effect etc.) to auditory systems, vocal tract morphology and other related aspects of physiology/neurology including, but not limited to, the thoracic nerve bundle (controlling diaphragm and chest wall muscles), hypoglossal nerve (controlling the tongue and articulatory space), hyoid bone, ear canals and physiology relating to vocal segmentation and breath control (for a review of physiology related to vocal evolution see Dunbar, 2016, p.2). Put simply, pre-linguistic humour involved communicating through vocalizations, gestures, and facial expressions, and the rewards and benefits of humour would have ensured the proliferation of such expressions and favoured the transmission of biologically related aspects by genetic, epigenetic, and cultural means. Humour related neophilia and the suite of positive feedback loops that has already discussed would have served to facilitate and diversify this process.

In addition to the preceding list of sensory-motor aspects, voluntary humorous behaviour would also have stimulated increased levels of dopamine production, which in turn, would have had the potential to have played a positive role in the emergence of language (Previc, 1999). This view is supported by Raghanti et al.'s assertion "The dopaminergic innervation of the striatum has been implicated in learning processes and in the development of human speech and language" (2016 p.2117). In specific genetic terms, both the FOXP2 gene (see p.213) and the (7R) allele of DRD4 gene (connected with neophilia and pro-social behaviour) (see pp.161-162) have already been mentioned and their replication would have been favoured due to enhanced sexual selection dynamics associated with humour. In sum, it can be seen that pre-linguistic voluntary humour production and appreciation served to beneficially evolve a variety of biological aspects relating to the neuro-physiology of action/perception systems, discrimination of audio and visual patterns and the biomechanics involved in the production of vocalizations, gestures and facial expressions, thus making the emergence of language biologically/physiologically feasible.

[158] There would also have been sensory-motor effects caused by to the social/behavioural ramifications of humour (neophilia, increased sociality etc.) but these will not be examined.

ii) Voluntary humour in relation to the conceptual-intentional system

In addressing the role of voluntary humour in relation to the conceptual-intentional system it must first be emphasized that the following is a highly abbreviated summary and for a comprehensive picture this thesis should be reviewed in its entirety. Before addressing aspects of the Chomskyan model it is worth noting that in general terms, voluntary humour would have enhanced the speed of cognitive processing of communicative expressions (Katz, 1993) and stimulated the evolution of this faculty as is implicit in the following statement by Suslov "(t)he biological function of a sense of humour consists in quickening the transmission of processed information into consciousness[159] and in a more effective use of brain resources" (1992 p.242). In relation to Chomskyan theory, I will first address the specific categories outlined by Hauser et al. 2002[160] and then, for the sake of efficiency, simply provide a point form list of additional aspects of the conceptual-intentional system relating directly to language that would have been enhanced by pre-linguistic voluntary humour production and appreciation.

In terms of Theory of Mind (see pp.85-86), a strong correlation with humour exists. Humour has been cited as a tool in developing Theory of Mind in early childhood development (Mireault et al., 2012; Reddy, 2008) and it is predicated on joint attention, which has been proposed to be a precursor to Theory of Mind in ontogenic development (Camaioini, 1992; Tomasello, 1995). It has also been proposed that "joint attention, play, and imitation, and language, might form part of a shared social-communicative representational system in infancy that becomes increasingly specialised and differentiated as development progresses" (Charman et al., 2000 p.481), which is significant in that humour evolved out of play (see pp.54-55) and involved imitation as well as joint attention. The important role that humour has in the ontogenic development of Theory of Mind can be seen as resulting in part from the role that Theory of Mind plays in the operation of humour itself. Lefcourt sums this up when he connects humour/laughter with "the ability to perceive the state of mind of the person or creature with whom one is in communication and with that of the object or target of the joke" (Lefcourt, 2001 p.45). Numerous scholars (e.g. Howe 2002; Jung, 2003; Leekham, 1991; Sullivan et al., 1995; Winner & Leekham, 1991) have

[159] It is interesting that Suslove specifically relates humour directly to consciousness.

[160] The categories are Theory of Mind; the capacity to acquire non-linguistic conceptual representations, use of referential vocal signals, the use of rational, intentional imitation; and voluntary control over signal production as evidence of intentional communication.

conducted research that supports the notion that humour and/or laughter involves second-order mental attribution (i.e. Theory of Mind), and humour also stimulates eye contact which has seen to directly activate Theory of Mind computations (Baron-Cohen, 1997; Kampe et al., 2003; Schilbach et al., 2006). As such, general humorous behaviour can be seen to have provided rewards and benefits for the engagement of the faculty of Theory of Mind, thus stimulating the evolution of this capacity and promoting transmission of any biologically related aspects by genetic and/or epigenetic means.

Similarly, a strong correlation can be seen between voluntary humour and the capacity to acquire non-linguistic conceptual representations in that any/all successful voluntary non-linguistic humorous expressions involved the transmission and acquisition of non-linguistic conceptual representations. This dynamic was central to the operation of humour. The creation of humour involved the distinguishing of specific aspects of perceptual and/or conceptual information by means of cross-correlation of information across multiple schemata and this process necessarily yielded abstracted, particulated conceptions. The expression of humour then shared such conceptions and subsequent to this, these conceptions had the potential to be accessed consciously or unconsciously in humorous or non-humorous (i.e. telic analogical thought and/or causal reasoning) contexts. As such, humorous expression would have involved the communication of information relating to abstracted concepts and their constituent elements, and yielded rewards and benefits. The reward aspect served to stimulate continued proliferation and hierarchical development, so humour not only incorporated the capacity to acquire non-linguistic conceptual representations into its essential mechanics, it also served to reward/stimulate this faculty, and facillitate transmission of any biologically related aspects by genetic and/or epigenetic means.

Referential vocal signals (as well as gestures and facial expressions) would have been used in voluntary humour and would have derived their incongruous aspect from novelty within intrinsic aspects, novelty within patterns, and the incorporation of existing signals in displaced contexts. In practical terms, humorous vocal expressions would have been vocalizations or combinations of vocalizations that were incongruous in their constituent properties, dynamics and/or in relation to context. Specific vocalizations could be associated with specific actions and/or facial expressions, thus rendering them cross-referential. Creating cross-referential incongruities would have been another potential source of humour i.e. manipulating patterns of referential vocal signals. As such, the multi-modal nature of humour facilitated the production of referential

vocal signals with intrinsic meaning. Associations would have been produced by imitation (e.g. of animal calls) or predicated by biological and cognitive constraints such as the association of high acoustic frequency with smallness and low acoustic frequency with largeness (Ohala et al., 1997). So it can be seen that there would have been a substantial number of referential vocal signals that could have been used in humorous expressions. Displacement of sound by vocal or other means was inherently incongruous and thus, potentially funny. Referential vocal calls of a telic nature from existing call systems (ie: warning calls, hunting signals) were, as a result, all potentially amusing in a displaced context involving positive emotional valence. As such they became domain-general rather than domain-specific, and any related information was cognitively processed in a manner that cross-correlated it with information across multiple schemata. This meant that the entire body of hominin vocal signals was subject to informatic and communicative restructuring. So it can be seen that humour was a platform for the autotelic manipulation of the full range of hominin referential vocal calls; it rewarded/stimulated such behaviour and promoted the transmission of any biologically related aspects by genetic and/or epigenetic means. In social/cultural terms, this created shared bodies of referential vocal calls that served to define individuals, societies and cultures, and in turn was then defined by them (see pp.141-154).

The rational, intentional imitation of animal calls and referential vocal calls in displaced context referred to in the last paragraph was indicative of the broader significance of imitation in voluntary humorous behaviour (see pp.87-88). Imitation is, in essence, the displacement of expression from one source to another, and as a manifestation of displacement, it tends to display incongruity and thus produce amusement. The inherent comic potential of imitation is further emphasized by Thorpe's definition of "true imitation" (see p.87), which cites novelty and improbability as constituent elements, both of which are associated with incongruity. It has been shown that higher apes have some capacity for imitation (Heyes, 1996; Whiten et al. 1996) but, lack the motivation to engage in it at a level that is quantitatively or qualitatively comparable to the level that is seen in modern humans. The proposed model shows that humour would have provided the necessary motivational impetus to help drive the imitative capacity to evolve to such levels. Imitation would have been an element of prelinguistic humour, as is reflected in its early appearance in childhood (McGhee, 1979) and the fact that it is a form of humour in and of itself (eg: Everts, 2003; Alford & Alford, 1981). It is proposed that, as a parallel to Heye's ontogenic notion, voluntary pre-linguistic humour served "the function of promoting the development of imitation…culturally evolved for the 'purpose' of expanding the range of action

units that children can imitate" (2016 p.4). This would likely have been a constituent part of a broader integrated system involving Theory of Mind, joint attention, analogical thought etc., and this would have created an evolutionary phylogenic dynamic similar to that created by the ontogenic "shared social-communicative representational system" proposed by Charman et al. (2000 p.481). In short, humorous behaviour rewarded/stimulated the imitative faculty in pre-linguistic hominins and promoted the transmission of any biologically related aspects by genetic and/or epigenetic means.

Voluntary control over signal production as evidence of intentional communication is the final aspect of the conceptual-intentional system cited by Hauser et al. and it is the easiest of all to reconcile with voluntary pre-linguistic humour. Voluntary control is, by definition, present in "voluntary" humour, and the process by which the voluntary aspect emerged was examined in step by step fashion (see pp.78-117), so no further extrapolation on this subject is required.

ii) Voluntary humour in relation to computational mechanisms for recursion

It has already been shown how recursion occurs in non-verbal humour (see pp.232-234), and voluntary humorous behaviour in hominins would have stimulated the hierarchical evolution of such recursive processes, but further consideration will be given to specific aspects cited by Hauser et al. In subdividing empirical approaches to the category "computational mechanisms for recursion" Hauser et al. list "sign or artificial language in trained apes and dolphins", "experiments with animals that explore the nature and content of number representation" and "models of the faculty of language that attempt to uncover the necessary and sufficient mechanisms" (2002, p.1573). These are all valid approaches but are not of value in the present task of relating the proposed model with the Chomskyan approach. The list also includes "spontaneous and training methods designed to uncover constraints on rule learning" and "shared mechanisms across different cognitive domains" (2002, p.1573) and these will now be discussed in relation to voluntary humour.

Hauser et al. claim that the computational mechanism of recursion is the only aspect of language that is unique to humans, but also point out that

> much of the complexity manifested in language derives from complexity in the peripheral components of FLB, especially those underlying the sensory-motor (speech

> or sign) and conceptual-intentional interfaces, combined with sociocultural and communicative contingencies... By contrast, according to recent linguistic theory, the computations underlying FLN may be quite limited (2002, p.1573).

In essence, recursion can be viewed as a relatively simple mechanism, but one of critical importance. I am not an expert in computational linguistics, but such expertise is not required in asserting the operation of the recursive mechanism in non-verbal humour; it is the operation of this mechanism in conjunction with the various complex elements in the construction and expression of language where such expertise is essential. In the context of this thesis, it is only necessary to assert the operation of recursion to the point where syntax begins to emerge.

The operation of merge as a fundamental aspect of the mechanics of humour has already been described (see p.96-97), as has the role of humour in the emergence of syntax (see pp.216-219). The recursive merge that operated in accidental humour would have involved:

- the processing of information derived from perception (a);
- the cross-correlation of (a) with information relating to an existing related conception (b);
- the configuration of a novel humorous conception (ab).

The novel humorous conception henceforth existed as a cognitive element that was distinct from the pre-existing conception of the subject, and its informatically parsed constituent elements, became a new part of the potential cognitive dynamics of future humorous events: each novel humorous conception helped to mediate the creation of further humorous conceptions ad infinitum. This, of course, was a simple form of recursion, but it was a functional aspect within a hierarchically evolving system. It was not a mere iterative loop but involved hierarchical progression, but because it applied to the fuzzy combinatory notion of concepts as well as their constituent elements, rather than to specific syntactic objects it was unwieldy in comparison to language, which involves specific discrete elements. Regardless of this, it created an informatic system that, driven by reward and mediated by biological, cognitive and social constraints, gradually identified and isolated specific elements within broader concepts and cross-correlated them to create novel concepts in a humorous framework or a telic one based on the process of analogical thought engendered by humour (see pp.118-121).

In practical terms, the emergence of voluntary humour introduced the use of specific gestures,

facial expressions and vocalizations ie: humorous expressions, and these, in turn, would have been employed in a recursive manner. Fuzzy perceptions/conceptions were replaced by specific communicative elements thus allowing the creation of discrete infinities drawn from a finite set. This is an interesting inversion if one considers that humour evolved from the informatic processing of concepts (ie:meaning) to the informatic processing of communicative elements, which were then reconfigured to create the system of language. Hurley et al. (2011) used the phrase "(u)sing humor to reverse engineer the mind" as the subtitle of their book discussing humour in an evolutionary context, but they failed to see the grand example that has just been outlined. Seen in relation to Feature Integration Theory (Treisman & Gelade, 1980)[161], humour served as a mechanism by which the constituent elements of holistic conceptions were informatically identified and parsed, and then used to create novel abstract conceptions which could then be shared with others in a communicative format.

In the earliest forms of voluntary humour, expressions would not have been syntactic in nature, but they would have gradually evolved to that point as was outlined in the discussion on the five elements of language (see pp.211-227). Put simply, discrete expressions could be combined, and variations in combinations of discrete expressions could be manipulated, in order to directly yield mutual rewards. As such, humour provided the drive and the mechanism to create syntactic objects. Its autotelic nature allowed for the communicative use of discrete arbitrary elements, and this system involved a hierarchically evolving recursive mechanism. As such, it can be seen that voluntary pre-linguistic humour fulfilled Hauser et al.'s requirement of "spontaneous and training methods designed to uncover constraints on rule learning" (2002, p.1573).

The final of Hauser et al.'s requirements is "shared mechanisms across different cognitive domains" (2002, p.1573), which conveniently brings the focus back to the notion of domain-generality. It has been asserted at numerous points in this thesis that the domain-general nature

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[161] Feature integration proposes that during the perception of a stimulus " features are registered early, automatically, and in parallel across the visual field, while objects are identified separately and only at a later stage, which requires focused attention" (Treisman & Gelade, 1980 p.98).

of humour is an essential component in the role it played in cognitive evolution. Humour is able to function within and across schemata (ie: intrinsic domains) such as language, music, numbers, facial recognition, it can be detected by all five senses, as well as within and across situational and/or behavioural domains (ie: extrinsic domains). Humour can be mediated by situations, activities, subjects or communicative modes but it remains domain-general, both intrinsically and extrinsically. Extrinsic domain-generality is important because recursive systems of thought are not sufficient in themselves to create modern human language. A recursive system of communication could, theoretically, use a finite number of devices to create an infinite number of expressions but if those expressions were locked within a specific behavioural domain they could potentially remain within that singular behavioural domain despite the "infinite" potential created by the recursive system. As long as the system was fulfilling its specific adaptive function it would have no reason to evolve any further. The extrinsic domain-generality of humour provided another level of infinity that allowed language to evolve as it did, and stimulation for this to occur was provided by rewards and humour related neophilia (see pp.158-164).

Hauser et al. offer support for this view of domain-generality when they state:

> During evolution, the modular and highly domain-specific system of recursion may have become penetrable and domain-general. This opened the way for humans, perhaps uniquely, to apply the power of recursion to other problems. This change from domain-specific to domain-general may have been guided by our particular selective pressures, unique to our evolutionary past, or as a consequence (by-product) of other kinds of neural reorganisation (2002 p.1578)

So, it can be seen that the proposed model not only fulfils the cross-domain criteria proscribed by Hauser et al., it also fulfils their prediction regarding domain-general thought and behaviour, though within the proposed model it was relaxed selection (see pp.64-65) rather than "selective pressures" that served as a catalyst.

10.4.3 Conclusions regarding the Chomskyan model

It can be seen that the proposed model provides a step by step evolutionary account for the development of the pre-requisites for the emergence of language as proscribed by Hauser et

al., 2002, including the sensory-motor system, a conceptual-intentional system, and the computational mechanisms for recursion. Furthermore, the process by which these conclusions were drawn was done in accordance with Tinbergen's (1963) four questions: issues relating to ontogeny, phylogeny, mechanism and adaptive significance have all been addressed in the course of this thesis. Consideration of Tinbergen's questions has provided valuable insight into psychological, behavioural, social, and ecological questions that the Chomskyan computational model has tended to overlook. Critical amongst the contributing factors in the operation of humour were the role of intrinsic and extrinsic domain-generality, paratelic functioning, and the role of rewards as a motivator, which circumvented the need for direct adaptive significance and thus provided a scenario where the use of arbitrary elements could emerge. The proposed model shows language to have emerged gradually (rather than saltationally) from a co-operative and co-evolving system of communication and computation involving the cognitive cross-correlation of information across multiple schemata and the use of communicative gestures, facial expressions and vocalizations. In relation to recursion, the type of recursion produced in pre-linguistic humour would have been more simplistic that which exists in language. It would have been more similar to grouping structure recursion that occurs in music as outlined by Jackendoff (2009), but this should not be seen as problematic. The proposed model is not intended to present pre-linguistic humour as a form of language, but to show that it significantly contributed in the evolution and synthesis of the pre-requisites of language. As such, it stands to reason that the type of recursion involved at this relatively early point would have exhibited a less evolved form than can be seen in language.

It is even possible to interpret Hauser et al. 2002 as presaging the proposed role of humour in the emergence of language. The paper states "FLN may have evolved for reasons other than language, hence comparative studies might look for evidence of such computations outside of the domain of communication (for example, number, navigation, and social relations)" (2002 p.1569). This statement is illustrative of the difficulty in removing communication entirely from the process and claiming a strictly computational origin of language, and Chomsky's collaboration with Hauser and Fitch was a step towards reconciling that difficulty. That said, humour fits very well into the "social relations" category that they have suggested. While Hauser et al.'s approach has been used in this thesis as the primary theory by which to examine the subject of the origin of language, there are also numerous other theories, some of which will now be briefly discussed in relation to the humour based theory being proposed.

10.5 Aspects from other origin of language theories

The preceding review of the proposed model in relation to Chomskyan theory was intended to provide a effective framework within which to consider the topic of the origin of language, but it does omit certain important issues/ideas relating to the origin of language. For the sake of brevity and clarity, I will simply address these in point form in alphabetical order. Some categories will have short additional notes, significant quotes, and/or page references.

Analogical thought and causal reasoning: The telic nature of the operation of language is evidence that an enhanced capacity for analogical thought and causal reasoning would have played a positive role in the emergence of language. While the critical role of the autotelic has been emphasized at many points, telic aspects of behaviour and their related cognitive processes would also have been essential (see pp.118-121).

Enhanced memory and processing speed: The positive role that an enhanced hominin capacity for memory acquisition and recall would play in the development of language is self evident. Humour's role in the engagement and enhancement of the faculty of memory has been discussed (see pp.89-91, and 160).

Motivation: This is an important behavioural element that has been emphasized by Hurford: "the key step to language was the innovative disposition to learn massive numbers of arbitrary symbols" (2004, p.551) (see pp.68-73).

Novelty/Creativity: Bickerton has said that in relation to the emergence of language "an important – maybe the most important – feature of information is its novelty...in contrast, ACSs (Animal Call Systems) endlessly repeat the same old signs for the same old situations- novelty would be disruptive, dysfunctional" (2009 p.48). Bickerton's use of the word "dysfunctional" is relevant to notion of the autotelic nature of humour as presented in this thesis in that they both propose evolutionary dynamics that transcend dynamics predicated strictly on adaptive value(s). See pp.158-164.

Socialization: There are many origin of language theories that claim a primary role for social interactions and social systems (eg: DiCarlo, 2010; Dunbar, 2003; Richerson & Boyd, 2010; Seyforth et al., 2005; Tomasello, 2009). The role of humour in the process of defining social

interactions, identities, and structures has been outlined in some detail in this thesis and as such, the proposed model accommodates, and is in agreement with, ideas that correlate sociality and the emergence of language (see pp.124-134 and 139-154).

Symbolic competence: "A disposition to acquire and use arbitrary elementary symbols in massive numbers characterizes humans no less than recursive syntax. And it is on the foundation of symbols that the recursive syntax of communicative language is built" (Hurford 2004, p.564). Other publications proposing an important role for symbolic competence include Brandon and Hornstein, 1986; Deacon, 1998; and Dickens & Dickens, 2001. The role of humour in the development of symbolic competence has been discussed (see pp.137-141).

Conclusions

In conclusion, the proposed model addresses the previously cited issues of intermediate stages in the appearance of language, the absence of existing languages more rudimentary than others, and the difficulty of finding a defensible story of adaptation. In regards to adaptation, it should, however, be noted that the proposed model transcends a traditional adaptive approach and attributes significant importance to rewards as well as adaptive benefits. This approach is supported by Piattelli-Palmarini's statement:

> since language and cognition probably represent the most salient and the most novel biological traits of our species, and since their present adaptive value has been constantly used as an explanation of their origins, it is now important to show that they may well have arisen from totally extra-adaptive mechanisms (1989 p.24).

The emphasis on "explanation" is the author's and is indicative of their criticism of the overemphasis on adaptive value in origin of language studies.

The proposed model is in agreement with Hurford's idea that language is not a "single monolithic behaviour" (2006 p.23) and shows it to have emerged in a gradual manner as the product of a co-operative and co-evolving cognitive/communicative system involving vocalizations, gestures and facial expressions. The role of humour in relation to the development of the five domains of language has been shown, and a step-by-step explanation for their proposed path of evolutionary development has been provided with consideration of

cognitive, biological and behavioural aspects. The autotelic nature of humour can be seen to have been essential in developing the capacity to manipulate discrete elements of language separately from holistic expressions. The proposed model has been discussed in relation to the Chomskyan framework for the origin of language put forward by Hauser et al. (2002) and can be seen to meet all their proscribed criteria. Positive correlations with other ideas within origin of language studies have also been shown.

11 Final summary

The purpose of this final summary is to:

- reiterate some of the ideas already expressed
- provide a cohesive overview of the material that has been covered
- consider strengths and limitations of the thesis
- discuss original contributions to knowledge
- suggest areas of future research. [162]

By this point all the ideas that are fundamental to this thesis should be familiar to the reader because information has been presented in the form of a hierarchical progression. As a result of this, once important aspects have been introduced, they have typically been reiterated, reconsidered and reconfigured with some frequency. As was discussed in the introduction, research related to behavioural aspects of hominin evolution is necessarily conjectural to some degree. This limitation should not be used as an excuse to neglect such research, but it does mean that supporting empirical evidence should be cited wherever possible and this thesis has consistently respected this maxim[163]. This is reflected in the substantial body of empirical evidence derived from both natural and social science research that has been referenced. In addition to this, there has been an effort to ensure that any research that has been cited which

[162] There will be no page references or citations in this section as their inclusion would be obtrusive and detrimental to clarity and flow.
[163] This can be related to the evolutionary dynamic of relaxed selection – as such, the thesis is the product of relaxed academic selection, which allows novel concepts to emerge, which a higher level of subsequent selection can then confirm or refute.

necessarily involves a degree of speculation (eg: evolutionary psychology, paleolinguistics) is similarly well grounded by supporting empirical evidence (cited works by Deacon, Dunbar, and Hauser et al. are good examples of this). Some examples of direct supporting empirical evidence are: the presence of the risorius muscle being limited to higher primates, the dating of the emergence of the seven-repeat (7R) allele of DRD4, humorous content in paleolothic art, and neophilic tendencies demonstrated in migratory patterns. In addition to this there is also a large body of supporting evidence that can be drawn from ontogenic/phylogenic parallels, the validity of which was asserted early in the thesis.

The subject of the emergence of humour and its possible role in the evolution of hominin cognition and resulting emergence of the aesthetic faculty and language has been examined bearing in mind biological, perceptual, cognitive, psychological, behavioural, communicative, social and cultural aspects in order to produce a comprehensive, holistic understanding of the subject(s). In the course of this examination it has been argued that the emergence of humour in hominin populations preceded the emergence of language for two primary reasons:

1) humour appreciation and production occurs at an earlier stage of ontogenic development than language;
2) humour can occur in more cognitively simplistic forms than language - it can be derived from the perception and cognition of incongruities in a situation of positive emotional valence, whereas language requires the construction of a mutual system of hierarchically organized arbitrary elements in a syntactic format.

Accepting this premise necessarily ascribes an important role to humour in the evolution of hominin cognition and communication because pre-linguistic humorous behaviour would have involved the cross-correlation of information across multiple schemata and the subsequent sharing of this information within the resulting domain-general communicative expressions: it would have been a communicative and informatic process. As such, humorous behaviour would have stimulated the use and development of the biological mechanisms underlying any/all related aspects of cognition and communication. Physiological, psychological and social rewards ensured that humorous behaviour was stimulated and proliferated. Physiological, psychological and social benefits ensured that humourous individuals were more likely to survive, reproduce and thus replicate any related genetic aspects.

There has been discussion on how the rewards stimulated by humour increased in number and broadened in nature as humorous behaviour proliferated, in part due to the psychological, social and cultural ramifications of such behaviour. This would have resulted in an interrelated suite of positive feedback loops operating in a generative hierarchical manner causing a positive upward spiral in the evolution of hominin cognition, behaviour, communication, sociality and culture**.** Due to the drive of rewards and the replicative enforcement of adaptive benefits, general humorous behaviour would have stimulated cognitive, behavioural, communicative, social, and cultural development, which would have stimulated further humorous behaviour etc. and this dynamic can be seen to have operated until such point when cognitive/communicative systems such as language and aesthetic creation/expression superceded it in importance.

The proposed scenario would have been facilitated by relaxed selection, prolonged childhood, and increased hominin brain size, though it is possible that humour emerged before brain expansion reached modern human levels. Humour is inherently social and as such, in an evolutionary context, it was a cognitively predicated process that utilized existing cognitive capacities and transfigured them into a social/communicative format that could operate across extrinsic domains. Voluntary humour functioned as a reward-driven, autocatalytic system that involved recursion as part of its fundamental operation, which contributed to humour's generative hierarchical dynamic and was significant in the emergence of language. Due to the roles of incongruity and humorous recall, humour would have been predicated on the perception/cognition of sameness and differences, and this dynamic would have stimulated the co-evolution of analogical thought and causal reasoning. The subjects of humour's possible role in the emergence/evolution of analogical thought and consciousness are complex ones that could only be touched on briefly in this thesis and it is suggested that further consideration and research in these areas is merited.

The proposed model shows a step by step homologous progression from the biologically based cause and effect system of tickling through to the cognitively based bio-social system of language. There has been some consideration of secondary ramifications of humorous behaviour in order to obtain a holistic picture showing the breadth of the relevant evolutionary dynamics. One good example of this is humour related neophilia, which can be seen to be substantially rooted in biology (i.e. the seven-repeat (7R) allele of DRD4 gene), is present at the levels of perception/cognition, is psychologically mediated, manifests itself in specific

behaviours, affects the content, frequency and styles of related communication, and has ramifications in terms of social relations and structures as well as collective culture.

In relation to the homologous evolution of cognitive and communicative aspects leading from humour to language, humour necessarily involved joint attention, face to face contact, imitation, vocalizations, gestures and other cognitive/behavioural elements that are relevant to the faculty of language amd would have contributed to the emergence of Theory of Mind. The origins of these aspects have been traced to higher apes and the dynamics by which humorous behaviour would have developed and integrated them has been discussed. This development of Theory of Mind, in turn, would have enhanced the potential for humorous interactions and this is representative of a generative, co-evolutionary dynamic. Similarly, the use of imitation and displacement in humorous behaviour would have enhanced hominin symbolic competence, which would then have enhanced the potential for humorous interactions. The autotelic nature of humour stimulated the development of behaviours and related cognition regardless of any adaptive value, which was significant in the emergence of discrete arbitrary communicative elements such as phonemes and morphemes. Emphasis has been placed on the relevance of the autotelic nature of humour in an evolutionary context, especially in relation to the potential for positive feedback loops that would have initiated and/or accelerated different aspects of hominin cognitive and social/behavioural evolution.

It has been asserted that while it is likely that the aesthetic impulse preceded language, the proposed model functions equally well even if this is not taken to be the case. In broader evolutionary terms, the emergence of the aesthetic impulse and language would have had a profound effect on the ramifications of humorous behaviour because language and aesthetic expression provided much more powerful and flexible tools for thought, expression and communication. Language, in particular, would have been immensely important and the adaptive significance of its use would have greatly eclipsed that which humour had previously offered. As such, language would have supplanted humour as the primary mode of communication. While language provided an advanced and efficient medium for humorous communication to operate within, its profoundly powerful and flexible telic potential would have greatly overshadowed the direct functions and effects of humorous behaviour. Humour's role as a generative force in the evolution of human cognition, communication, society and culture would have been substantially diminished. Following the emergence of language, it is possible that individuals limited to non-linguistic humour demonstrated an inability to adapt to telic

language based behaviour, and in such circumstances humour would have been a regressive trait.

In evolutionary terms, humour served as a both a pattern recognition and a “break in pattern” recognition system. As such, it served the informatic function of detecting and parsing constituent elements of holistic perceptions, and creating abstracted conceptions which could then be cross-correlated across multiple schemata and manifested in domain-general expressions. Such expressions then became part of shared bodies of knowledge imbued with social capital. Humour consituted an autotelic and autocatalytic system that stimulated the hierarchical evolution of hominin cognition, behaviour, communication, sociality and culture, before being largely supplanted in its importance by the aesthetic faculty and language, which were themselves products of this process. This represented a significant progression towards bio-social evolutionary dynamics for hominins, and it can be seen that the dynamics of the system of rewards triggered by humour marked a turning point in this regard.

In general terms, the view of humour in an evolutionary context that is presented, and more particularly, the role humour is proposed to have played in the emergence of symbolic competence, the aesthetic faculty and language, represents a new contribution of knowledge to the field. As was stated in the introduction, the intention of the research was to yield a deep and comprehensive understanding of the nature of humour and its role in hominin evolution. The fact that many novel academic approaches relating to a diversity of subjects were yielded was purely incidental to the task at hand. That said, it is worthwhile to list a few of the new contributions to knowledge that have been proposed/presented. The following provides a brief partial summary of these in no particular order.

i) A holistic picture of the role of humour in an evolutionary context rather than one based primarily on a single adaptive benefit, which outlines logical causal sequences based on specific biological, cognitive, social and behavioural aspects.

ii) The notion of humorous recall, which proposes that some humour processing is dependant primarily on memory recall rather than incongruity i.e. the cognitive processing of sameness rather than difference. Forabosco (1980) acknowledges this dynamic, (referring to it as familiarity) but provides no analysis regarding the fact that it is a dynamic within which there is no incongruity.

iii) The notion that emotional ambivalence in humour was derived in part from ambiguity created by the role of the silent bared-teeth display that preceded actual smiling, which resulted from the physiological constraints of laughter.

iv) The notion that humour first emerged in hominins as a neotenous behaviour. Relaxed selection allowed play to occur with older, more cognitively developed children and stimulated an increase in neural plasticity which facilitated the emergence of a more cognitively advanced form of smiling/laughter stimulus (i.e. humour). This scenario also provided an ideal environment for the continuation of such behaviour and related information to be shared between peers.

v) The notion that the role of rewards in the dynamics of humour created a suite of interconnected positive feedback loops that caused humour to stimulate, and be a constituent of, an auto-catalytic, generative system that served to evolve hominin physiological, cognitive, communicative, behavioural and social systems.

vi) The notion that the emergence and evolution of humour and role it played in hominin evolution was dependant on the rewards it yielded as well as the adaptive benefits that were yielded.

vii) Comprehensive lists of rewards and benefits that are yielded by humorous behaviour.

viii) The notion that humorous behaviour in hominins stimulated the evolution of imitative behaviour and the capacity for analogical thought and causal reasoning, as well as memory acquisition, retention and recall, both qualitatively and quantitatively. Collectively, these and other factors indicate that humorous behaviour played an important role in the development of Theory of Mind.

ix) The notion that humour enhanced the ability of hominin individuals to perceive and regulate emotions in others by way of communicative expression, which in turn, would have enhanced co-operation and engendered pro-sociality.

x) The notion that humour introduced an autocatalytic system involving social learning and the creation and transmission of domain-general information which facilitated the emergence of the hominin capacity for voluntary, cross-correlation of information between multiple schemata i.e. meta-cognition.

xi) The notion that humour fostered an emotional climate in hominins that had the potential to enhance the capabilities and phenomenological experiences of the less social individuals and contributed to greater social integration of individuals with perceptible physical and psychological anomalies.

xii) The notion that increased sociality through humour in hominins engendered a situation of relaxed selection, which lead to an increased level of genetic/phenotypic plasticity in hominin populations.

xiii) The notion that general humorous expression provided the first medium by which individuals and groups could voluntarily and creatively affect social statuses and dynamics and thus transcend the previously existing dynamics that were dictated primarily by biological factors.

xiv) The notion that humour was the first form of hominin aesthetic expression and as such, the aesthetic faculty emerged from an affectively mediated reflex based on biologically predicated cognitive functioning.

xv) The notion that an evolutionary path from autotelic to telic was essential for the emergence of language because language would have required the cognitive identification, isolation, and abstraction of singular elements within a communicative system. Humour provided a system incorporating this, which explains why there was the development of arbitrary, constituent elements devoid of independent telic function and/or adaptive significance.

xvi) The notion that pre-linguistic humour would have involved the use of phonemes, morphemes, syntax, semantics and pragmatics, and together with the capacities for analogical thought and causal reasoning that humour engendered. There was a gradual integration of these aspects into a coordinated hierarchical system, which resulted in the emergence of language[164].

xvii) The notion that humorous behaviour served to initiate the conscious identification, communication and consolidation of taboos in hominin societies.

xviii) The notion that humorous behaviour stimulated the imitative faculty in hominins and in so doing contributed to the proliferation of mirror neurons by way of Hebbian learning.

As a result of the preceding points as well as the proposed model in general, it is my hope that this thesis will stimulate further research and debate in terms of how humour is defined, the role it played in hominin evolution, and what role it might play in ontogenic development, including

[164] The preceding list is only a partial one and a complete reading of the thesis is required in order to get a full understanding of the original contributions to knowledge that are involved.

the emergence of language and the aesthetic faculty. It has been suggested within this thesis that there are courses of research that would be valuable in furthering knowledge of the subject(s) in question. The following list provides a partial summary of these.

i) Research to determine whether or not laughter stimulates oxytocin production. Existing indirect evidence suggests that it is reasonable to believe this may be the case. If clinical research can confirm this correlation, it will provide further biological evidence that supports the proposed model and it also may have ramifications related to humour therapies. Similarly, there would also be value in research relating humour/laughter to other neurochemical activity (eg: vasopressin, pheromones, GABA).
ii) Research into the relationship between humour and analogical thought/causal reasoning in early childhood development and/or in higher apes. It has been proposed that humorous behaviour facilitated the emergence of analogical thought and causal reasoning, and such research could help to confirm or deny this and/or determine the specific mechanics and dynamics of such processes.
iii) Research into humour in relation to the seven-repeat (7R) allele of DRD4 to help to determine what correlations might exist. If correlations do exist then genetic evidence from hominin remains may be used as a rough guide to determine when/where humorous behaviour may have first emerged and/or proliferated.
iv) Research on the role of humour during pregnancy with emphasis on possible therapeutic aspects to mitigate psychological and physiological adversity.
v) Research into possible interrelationships between humour, the aesthetic faculty, and the development of analogical thought, which could be done in relation to early childhood development. A greater level of knowledge in this area could contribute to a more complete understanding of both ontogenic and phylogenic dynamics.
vi) Research into the possibility of an increase in genetic markers occurring in the fossil record indicating phenotypic variation correlating with the proposed timeline for humour[165]. This should show an increase beginning around 50KYA in conjunction with the emergence of the seven-repeat (7R) allele of the DRD4 gene.

[165] Timeline: 1.9 MYA dopamine production → 0.8 – 1.2 MYA extended childhood → 160 KYA brain development at modern levels → 40 to 50 KYA 7r allele of DRD4 emerges. This implies gradual neotenous introduction of humour

vii) Research into the effects of humour, laughter and smiling on epigenetics related to the FOXP2 gene.

It is also suggested that further research regarding the possible use of humour therapies in the treatment of childhood autism and childhood language acquisition deficits is merited, as well as research related to the pedagogical potential of humour in pre-linguistic stages of infant development. Because the thesis presents a model explaining the origin of many of the fundamental aspects of human cognition, as well as the aesthetic impulse and language, it necessarily has the potential to affect the way these subjects are considered by future scholars and could stimulate novel research approaches. The development of Artificial Intelligence models based on evolutionary recapitulation could possibly benefit in this regard.

As a theoretical work built substantially on evidence-based research, there is potential for this thesis to stimulate further ideas and debate, and this, in conjunction with advances in technology associated with related research may help to produce a clearer picture of how the modern human condition emerged, and what humour's role in that process was.

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between 1 MYA and 160 KYA, followed by a rapid increase around 50 KYA which correlates with rates of cultural evolution described by Mithen.

12 Bibliography

Abel, E.L. and Kruger, M.L., 2010. Smile intensity in photographs predicts longevity. *Psychological Science*, *21*(4), pp.542-544.

Abel, M.H., 2002. Humor, stress, and coping strategies. *Humor–International Journal of Humor Research*, *15*(4), pp.365-381.

Adang, O.M., 1986. Exploring the social environment: A developmental study of teasing in chimpanzees. *Ethology*, *73*(2), pp.136-160.

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B. and Gabrieli, J.D., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron*, *50*(3), pp.507-517.

Addison, J., 1712. *The Spectator,* 494 (26 September 1712).

Agrawal, A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. *Science*, *294*(5541), pp.321-326.

Aitchison, J., 1996. *The seeds of speech: Language origin and evolution*. Cambridge, Cambridge University Press.

Alexander, J.C., Eyerman, R., Giesen, B., Smelser, N.J. and Sztompka, P., 2004. *Cultural trauma and collective identity*. Ewing, New Jersey, University of California Press.

Alexander, R.D., 1989. Evolution of the human psyche. *The human revolution: Behavioural and biological perspectives on the origins of modern humans*. Edinburgh, Edinburgh University Press, pp.455-513.

Alexander, R.D., Noonan, K.M. and Crespi, B.J., 1991. The evolution of eusociality. *The biology of the naked mole-rat*. Princeton, Princeton University Press, p.44.

Alford, F. and Alford, R., 1981. A Holo-Cultural Study of Humor. *Ethos*, *9*(2), pp.149-164.

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L., 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), pp.485-488.

Allman, J.M., Tetreault, N.A., Hakeem, A.Y., Manaye, K.F., Semendeferi, K., Erwin, J.M., Park, S., Goubert, V. and Hof, P.R., 2010. The von Economo neurons in frontoinsular and anterior cingulate cortex in great apes and humans. *Brain Structure and Function*, *214*(5-6), pp.495-517.

Als, H., Duffy, F.H., McAnulty, G.B., Rivkin, M.J., Vajapeyam, S., Mulkern, R.V., Warfield, S.K., Huppi, P.S., Butler, S.C., Conneman, N. and Fischer, C., 2004. Early experience alters brain function and structure. *Pediatrics*, *113*(4), pp.846-857.

Amaki, M., Kamide, K., Takiuchi, S., Niizuma, S., Horio, T. and Kawano, Y., 2007. A case of neurally mediated syncope induced by laughter successfully treated with combination of propranolol and midodrine. *International heart journal*, *48*(1), pp.123-127.

Anati, E., 1956. Rock Engravings from the Jebel Ideid (Southern Negev). *Palestine Exploration Quarterly*, *88*(1), pp.5-13.

Angulo, J.C. and García-Díez, M., 2009. Male genital representation in Paleolithic art: erection and circumcision before history. *Urology*, *74*(1), pp.10-14.

Apte, M.L., 1985. *Humor and laughter: An anthropological approach*. Ithaca, N.Y., Cornell University Press

Apter, M.J. and Smith, K.C.P., 1977. Humour and the theory of psychological reversals. In *It's a funny thing, humour-International conference on humour & laughter,* pp. 95-100.

Apter, M.J., 1989. *Reversal theory: Motivation, emotion and personality*. London, Taylor & Frances/Routledge.

Araya-Salas, M., 2012. Is birdsong music? Evaluating harmonic intervals in songs of a Neotropical songbird. *Animal Behaviour*, *84*(2), pp.309-313.

Arbib, M.A., Liebal, K., Pika, S., Corballis, M.C., Knight, C., Leavens, D.A., Maestripieri, D., and Tanner, J.E., 2008. Primate vocalization, gesture, and the evolution of human language. *Current anthropology*, *49*(6), pp.1053-1076.

Arcadi, A.C., Robert, D. and Boesch, C., 1998. Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates*, *39*(4), pp.505-518.

Archakis, A. and Tsakona, V., 2005. Analyzing conversational data in GTVH terms: A new approach to the issue of identity construction via humor. *Humor-International Journal of Humor Research*, *18*(1), pp.41-68.

Arculus, C., 2011. Communicative Musical Funniness. In *MERYC 2011: Proceedings of the 5th Conference of the European Network of Music Educators and Researchers of Young Children,* pp. 33-41.

Aristotle. *The Poetics*. Online source: http://www.online-literature.com/aristotle/poetics/5/

Armstrong, D.F. and Wilcox, S., 2007. *The gestural origin of language*. Oxford, Oxford University Press.

Armstrong, D.F., Stokoe, W.C. and Wilcox, S.E., 1995. *Gesture and the nature of language*. Cambridge, Cambridge University Press.

Arnason, U., Gullberg, A., Burguete, A.S. and Janice, A., 2001. Molecular estimates of primate divergences and new hypotheses for primate dispersal and the origin of modern humans. *Hereditas*, *133*(3), pp.217-228.

Arnold, S.J., 1983. Sexual selection: the interface of theory and empiricism. *Mate choice*, pp.67-107.

Asad, T., 1986. The concept of cultural translation in British social anthropology. *Writing culture: The poetics and politics of ethnography*, *1*, pp.141-164.

Ashby, F.G. and Isen, A.M., 1999. A neuropsychological theory of positive affect and its influence on cognition. *Psychological review*, *106*(3), p.529.

Ashforth, B.E. and Mael, F., 1989. Social identity theory and the organization. *Academy of management review*, *14*(1), pp.20-39.

Attardo, S. and Pickering, L., 2011. Timing in the performance of jokes. *Humor-International Journal of Humor Research*, *24*(2), pp.233-250.

Attardo, S. and Raskin, V., 1991. Script theory revis (it) ed: Joke similarity and joke representation model. *Humor-International Journal of Humor Research*, *4*(3-4), pp.293-348.

Attardo, S., 2003. Introduction: the pragmatics of humor. *Journal of Pragmatics*, *35*(9), pp.1287-1294.

Aubert, M., Brumm, A., Ramli, M., Sutikna, T., Saptomo, E.W., Hakim, B., Morwood, M.V., van den Bergh, G.D., Kinsley, L. and Dosseto, A., 2014. Pleistocene cave art from Sulawesi, Indonesia. *Nature*, *514*(7521), pp.223-227.

Avolio, B.J., Howell, J.M. and Sosik, J.J., 1999. A funny thing happened on the way to the bottom line: Humor as a moderator of leadership style effects. *Academy of Management Journal*, *42*(2), pp.219-227.

Azim, E., Mobbs, D., Jo, B., Menon, V. and Reiss, A.L., 2005. Sex differences in brain activation elicited by humor. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(45), pp.16496-16501.

Badyaev, A.V., 2009. Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1520), pp.1125-1141.

Bahn, P.G., 1998. *The Cambridge illustrated history of prehistoric art*. Cambridge, Cambridge University Press.

Bainum, C.K., Lounsbury, K.R. and Pollio, H.R., 1984. The development of laughing and smiling in nursery school children. *Child Development*, pp.1946-1957.

Baldanzi, S., McQuaid, C.D., Cannicci, S. and Porri, F., 2013. Environmental domains and range-limiting mechanisms: testing the abundant centre hypothesis using Southern African sandhoppers. *PloS one*, *8*(1), p.e54598.

Baldwin, D.A., 1995. *Understanding the link between joint attention and language.* In C. Moore & P.J. Dunham (Eds.) Joint attention: Its origins and role in development. Hillsdale, NJ: Erlbaum, pp.131-158.

Baldwin, J.R., Faulkner, S.L. and Hecht, M.L., 2006. A moving target: The illusive definition of culture. *Redefining culture: Perspectives across the disciplines*. London, Routledge, pp.3-26.

Balter, M., 2004. Seeking the key to music. *Science*, *306*(5699), pp.1120-1122.

Bandura, A., 1971. Social learning theory. New York, General Learning Press.

Bandura, A., 1997. *Self-efficacy: The exercise of control*. New York, Worth Publishers.

Bandura, A., 1999. Social cognitive theory: An agentic perspective. *Asian Journal of Social Psychology*, *2*(1), pp.21-41.

Bar-Yosef, O., 1998. On the nature of transitions: the Middle to Upper Palaeolithic and the Neolithic Revolution. *Cambridge Archaeological Journal*, *8*(2), pp.141-163.

Bar-Yosef, O., 2002. The upper paleolithic revolution. *Annual Review of Anthropology*, *31*(1), pp.363-393.

Barbieri, F. and Saggion, H., 2014. Automatic Detection of Irony and Humour in Twitter. In *ICCC,* pp. 155-162.

Bard, K.A., 1994. Evolutionary roots of intuitive parenting: Maternal competence in chimpanzees. *Infant and Child Development*, *3*(1), pp.19-28

Bardo, M.T., Donohew, R.L. and Harrington, N.G., 1996. Psychobiology of novelty seeking and drug seeking behavior. *Behavioural brain research*, *77*(1), pp.23-43.

Barkow, J.H., 1989. *Darwin, sex, and status: Biological approaches to mind and culture*. Toronto, University of Toronto Press.

Barlow, H.B., 1980. Nature's joke: A conjecture on the biological role of consciousness. In Brian Josephson & V. Ramach (eds.), *Consciousness and the Physical World*. London, Pergamon Press.

Baron-Cohen, S., 1997. *Mindblindness: An essay on autism and theory of mind*. Cambridge, Mass., MIT Press.

Baron-Cohen, S., 1999. The evolution of a theory of mind. In Corballis, M, & Lea, S (eds), *The descent of mind: psychological perspectives on hominid evolution.* Oxford, Oxford University Press.

Barrett, H. and Kurzban, R., 2006. Modularity in cognition: framing the debate. *Psychological review*, *113*(3), p.628.

Barton, R.A. and Dunbar, R.I., 1997. Evolution of the social brain. *Machiavellian intelligence II: Extensions and evaluations*, *2*, p.240.

Bates, E., 1993. Modularity, domain-specificity and the development of language. *Discussions in Neuroscience*, *10*(1), pp.136-148.

Baumeister, R.F., 2000. Gender differences in erotic plasticity: the female sex drive as socially flexible and responsive. *Psychological Bulletin*, *126*(3), p.347.

Bayliss, D.M., Jarrold, C., Gunn, D.M. and Baddeley, A.D., 2003. The complexities of complex span: explaining individual differences in working memory in children and adults. *Journal of Experimental Psychology: General*, *132*(1), p.71.

Beattie, J., 1776. *An Essay on Laughter and Ludicrous Composition, Written in the Year 1764*. Edinburgh, W. Creech and E. and C. Dilly.

Bednarik, R.G., 2009. The global context of Lower Palaeolithic Indian palaeoart. *Man and Environment*, *34*(2), pp.1-16.

Bednarik, R. G., 2011. *The human condition*. New York, Springer Science & Business Media.

Bednarik, R.G., 2013. Myths about rock art. *Journal of Literature and Art Studies*, *3*(8), pp.482-500.

Belayachi, S., Laloyaux, J., Larø i, F. and Van der Linden, M., 2015. Internal Encoding Style and Schizotypy: Toward a Conceptually Driven Account of Positive Symptoms. *Journal of Personality Disorders*, *29*(3), pp.303-315.

Bell, N.J., McGhee, P.E. and Duffey, N.S., 1986. Interpersonal competence, social assertiveness and the development of humour. *British Journal of Developmental Psychology*, *4*(1), pp.51-55.

Benitez-Bribiesca, L., 2001. Memetics: A dangerous idea. *Interciencia*, *26*(1), pp.29-31.

Bennett, M.P., Zeller, J.M., Rosenberg, L. and McCann, J., 2003. The effect of mirthful laughter on stress and natural killer cell activity. *Alternative therapies in health and medicine*, *9*(2), p.38.

Berg, D.V. and Van Brockern, S., 1995. Building Resilience through Humor. *Reclaiming Children and Youth: Journal of Emotional and Behavioral Problems*, *4*(3), pp.26-29.

Bergen, D., 2003. Theories of pretence, mental rerepresentation, and humor development. *Contemporary perspectives on play in early childhood education*, p.41.

Bergen, D., 2007. Humor as a facilitator of social competence in early childhood. *Contemporary perspectives on research in socialization and social development, ed. B. Spodek and ON Saracho*, pp.19-38.

Bergman, K., Sarkar, P., O'connor, T.G., Modi, N. and Glover, V., 2007. Maternal stress during pregnancy predicts cognitive ability and fearfulness in infancy. *Journal of the American Academy of Child & Adolescent Psychiatry*, *46*(11), pp.1454-1463.

Bergson, H., Brereton, C.S.H. and Rothwell, F., 1911. *Laughter: An essay on the meaning of the comic*. London, Macmillan.

Berk, L., Cavalcanti, P. and Bains, G., 2012. EEG brain wave band differentiation during a eustress state of humor associated mirthful laughter compared to a distress state. *The FASEB Journal*, *26*(1 Supplement), pp.709-1.

Berk, L., Felten, D.L., Tan, S.A., Bittman, B.B. and Westengard, J., 2001. Modulation of neuroimmune parameters during the eustress of humor-associated mirthful laughter. *Alternative therapies in health and medicine*, *7*(2), p.62.

Berk, L., Tan, S. and Fry, W., 1993. Eustress of humor associated laughter modulates specific immune system components. *Annals of behavioral medicine*, *15*, p.S111.

Berk, L., Tan, S., Fry, W., Napier, B.J., Lee, J.W., Hubbard, R.W., Lewis, J.E. and Eby, W.C., 1989. Neuroendocrine and stress hormone changes during mirthful laughter. *The American journal of the medical sciences*, *298*(6), pp.390-396.

Berk, R.A., 2001. The active ingredients in humor: Psychophysiological benefits and risks for older adults. *Educational Gerontology*, *27*(3-4), pp.323-339.

Berlyne, D.E., 2014. *Conflict Arousal and Curiosity*. Manfield Centre, CT: Martino Publishing

Berlyne, D.E., 1972. Humor and its kin. *The psychology of humor: Theoretical perspectives and empirical issues*, New York, Academic Press, pp.43-60.

Bickerton, D., 1990. *Species and language.* Chicago, University of Chicago Press.

Bickerton, D., 1992. *Language and species*. Chicago, University of Chicago Press.

Bickerton, D., 1996. *Language and human behaviour*. London, University College Press.

Bickerton, D., 2003. Symbol and structure: a comprehensive framework for language evolution. *Studies in the Evolution of Language*, *3*, pp.77-93.

Bickerton, D., 2009. *Adam's tongue: how humans made language, how language made humans*. New York, Hill and Wang.

Bickerton, D., 2016. *Roots of language*. Ann Arbor, Michigan, Karoma Publishers.

Bishop, D.V.M., 2009. Genes, cognition, and communication. *Annals of the New York Academy of Sciences*, *1156*(1), pp.1-18.

Bisley, J.W. and Goldberg, M.E., 2003. Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*(5603), pp.81-86.

Black, D.W., 1982. Pathological laughter: a review of the literature. *The Journal of nervous and mental disease*, *170*(2), pp.67-71.

Blackmore, S., 2000. The power of memes. *Scientific american*, *283*(4), pp.52-61.

Blackmore, S., 2001. Evolution and memes: The human brain as a selective imitation device. *Cybernetics & Systems*, *32*(1-2), pp.225-255.

Blakemore, S.J., Wolpert, D. and Frith, C., 2000. Why can't you tickle yourself?. *Neuroreport*, *11*(11), pp.R11-R16.

Bliss, S.H., 1915. The origin of laughter. *The American Journal of Psychology*, *26*(2), pp.236-246.

Bloch, M., 2000. A well-disposed social anthropologist's problems with memes. In *Darwinizing culture, ed. R. Aunger*. Don Mills, Canada, Oxford University Press U.S.A, pp.189-204.

Block, N., 1995. Some concepts of consciousness. *Sciences*, *18*(2).

Boero, D.L., 1992. Alarm calling in Alpine marmot (Marmota marmota L.): evidence for semantic communication. *Ethology ecology & evolution*, *4*(2), pp.125-138.

Bogin, B., 1997. Evolutionary Hypotheses for Human Childhood. *Yearbook of Physical Anthropology* 40: 63–89.

Bonanno, G.A., Keltner, D., Noll, J.G., Putnam, F.W., Trickett, P.K., LeJeune, J. and Anderson, C., 2002. When the face reveals what words do not: facial expressions of emotion, smiling, and the willingness to disclose childhood sexual abuse. *Journal of personality and social psychology*, *83*(1), p.94.

Bonari, L., Pinto, N., Ahn, E., Einarson, A., Steiner, M. and Koren, G., 2004. Perinatal risks of untreated depression during pregnancy. *The Canadian Journal of Psychiatry*, *49*(11), pp.726-735.

Borenstein, E. and Ruppin, E., 2005. The evolutionary link between mirror neurons and imitation: An evolutionary adaptive agents model. *Behavioral and Brain Sciences*, *28*(2), pp.127-128.

Botha, R., 2009. On musilanguage/"Hmmmmm" as an evolutionary precursor to language. *Language & Communication*, *29*(1), pp.61-76.

Bouissac, P., 2015. *The semiotics of clowns and clowning: rituals of transgression and the theory of laughter.* London, Bloomsbury.

Bourdieu, P., 1984. *Distinction: A social critique of the judgement of taste*. Cambridge, Ma., Harvard University Press.

Bourdieu, P., 1989. Social space and symbolic power. *Sociological theory*, *7*(1), pp.14-25.

Bourdieu, P., 2011. The forms of capital.(1986). *Cultural theory: An anthology*, *1*, pp.81-93.

Bourhis, R.Y., Gadfield, N.J., Giles, H. and Tajfel, H., 1977. Context and ethnic humour in intergroup relations. In *It's a funny thing, humor, eds. Chapman, A. & Foot, H.*. New York, Pergamon Press, pp.261-265.

Bourke, A.F.G.,1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol. 12*, pp.245–257.

Boyd, B., 2004. Laughter and literature: A play theory of humor. *Philosophy and literature*, *28*(1), pp.1-22.

Boyd, R. and Richerson, P.J., 1996, January. Why culture is common, but cultural evolution is rare. In *Proceedings-British Academy* (Vol. 88, pp. 77-94). Oxford, Oxford University Press Inc..

Boyer, P., 2000. *Evolution of the modern mind and the origins of culture: Religious concepts as a limiting case* (pp. 93-112). Cambridge, Cambridge University Press.

Bragg, M.J., 2006. Fall about laughing: a case of laughter syncope. *Emergency Medicine Australasia*, *18*(5-6), pp.518-519.

Brand, R.J., Baldwin, D.A. and Ashburn, L.A., 2002. Evidence for 'motionese': modifications in mothers' infant-directed action. *Developmental Science*, *5*(1), pp.72-83.

Brandon, R.N. and Hornstein, N., 1986. From icons to symbols: Some speculations on the origins of language. *Biology and Philosophy*, *1*(2), pp.169-189.

Brant, C.S., 1948. On joking relationships. *American Anthropologist*, *50*(1), pp.160-162.

Bregman, A.S., 2008. Auditory scene analysis. *The senses: A comprehensive reference*, *3*, pp.861-870.

Bregman, A.S., 1994. *Auditory scene analysis: The perceptual organization of sound*. Cambridge, Ma., MIT Press.

Bressler, E.R. and Balshine, S., 2006. The influence of humor on desirability. *Evolution and Human Behavior*, *27*(1), pp.29-39.

Bressler, E.R., Martin, R.A. and Balshine, S., 2006. Production and appreciation of humor as sexually selected traits. *Evolution and Human Behavior*, *27*(2), pp.121-130.

Bretherton, I. and Beeghly, M., 1982. Talking about internal states: The acquisition of an explicit theory of mind. *Developmental psychology*, *18*(6), p.906.

Brône, G., Feyaerts, K. and Veale, T., 2006. Introduction: Cognitive linguistic approaches to humor. *Humor–International Journal of Humor Research*, *19*(3), pp.203-228.

Brousseau, L., Malcuit, G., Pomerleau, A. and Feider, H., 1996. Relations between lexical-temporal - atures in mothers' speech and infants' interactive behaviours. *First Language*, *16*(46), pp.41-59.

Brown, K.E. and Penttinen, E., 2013. "A 'sucking chest wound is nature's way of telling you to slow down….": humour and laughter in war time. *Critical Studies on Security*, *1*(1), pp.124-126.

Brown, S., 2000. Evolutionary models of music: From sexual selection to group selection. In *Perspectives in ethology* (pp. 231-281). New York, Springer U.S..

Brown, S., 2001. Are music and language homologues?. *Annals-New York Academy of Sciences*, *930*, pp.372-374.

Brown, S., 2007. Contagious heterophony: a new theory about the origins of music. *Musicae Scientiae*, *11*(1), pp.3-26.

Brownell, H.H., Michel, D., Powelson, J. and Gardner, H., 1983. Surprise but not coherence: Sensitivity to verbal humor in right-hemisphere patients. *Brain and language*, *18*(1), pp.20-27.

Brüne, M., 2000. Neoteny, psychiatric disorders and the social brain: Hypotheses on heterochrony and the modularity of the mind. *Anthropology & Medicine*, *7*(3), pp.301-318.

Brüne, M. and Brüne-Cohrs, U., 2006. Theory of mind—evolution, ontogeny, brain mechanisms and psychopathology. *Neuroscience & Biobehavioral Reviews*, *30*(4), pp.437-455.

Brutsche, M.H., Grossman, P., Müller, R.E. and Wiegand, J., 2008. Impact of laughter on air trapping in severe chronic obstructive lung disease. *International journal of chronic obstructive pulmonary disease*, *3*(1), p.185.

Bryant, P.E., Bradley, L., Maclean, M. and Crossland, J., 1989. Nursery rhymes, phonological skills and reading. *Journal of Child language*, *16*(2), pp.407-428.

Bucaria, C. and Barra, L., 2016. Taboo Comedy on Television: Issues and Themes. In *Taboo Comedy, eds. Bucaria, C. and Barra, L.*. London, Palgrave Macmillan U.K., pp. 1-18.

Buchowski, M.S., Majchrzak, K.M., Blomquist, K., Chen, K.Y., Byrne, D.W. and Bachorowski, J.A., 2007. Energy expenditure of genuine laughter. *International journal of obesity (2005)*, *31*(1), p.131.

Buchsbaum, D., Bridgers, S., Weisberg, D.S. and Gopnik, A., 2012. The power of possibility: Causal learning, counterfactual reasoning, and pretend play. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1599), pp.2202-2212.

Bunzeck, N., Doeller, C.F., Fuentemilla, L., Dolan, R.J. and Duzel, E., 2009. Reward motivation accelerates the onset of neural novelty signals in humans to 85 milliseconds. *Current Biology*, *19*(15), pp.1294-1300.

Burke, P.J. and Reitzes, D.C., 1981. The link between identity and role performance. *Social psychology quarterly*, pp.83-92

Burrows, A.M., Waller, B.M., Parr, L.A. and Bonar, C.J., 2006. Muscles of facial expression in the chimpanzee (Pan troglodytes): descriptive, comparative and phylogenetic contexts. *Journal of anatomy*, *208*(2), pp.153-167.

Buss, D. M., 1991. Evolutionary personality psychology. *Annual Review of Psychology, 42*, pp.459-491.

Butovskaya, M.L. and Kozintsev, A.G., 1996. A neglected form of quasi-aggression in apes: Possible relevance for the origins of humor. *Current Anthropology*, *37*(4), pp.716-717.

Butterworth, G., 1999. *Neonatal imitation: Existence, mechanisms and motives*. Cambridge, Cambridge University Press.

Byrne, R.W., 2007. Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1480), pp.577-585.

Caldwell, C.A. and Millen, A.E., 2008. Studying cumulative cultural evolution in the laboratory. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *363*(1509), pp.3529-3539.

Caldwell, C.A. and Millen, A.E., 2009. Social learning mechanisms and cumulative cultural evolution: is imitation necessary?. *Psychological Science*, *20*(12), pp.1478-1483.

Camaioni, L., 1992. Mind knowledge in infancy: The emergence of intentional communication. *Infant and Child Development*, *1*(1), pp.15-22.

Campbell, S., 2004. *Watch me grow: A unique, 3-dimensional week-by-week look at your baby's behavior and development in the womb*. London, Carroll and Brown Publishers.

Cann, A, Holt, K. and Calhoun, L.G., 1999. The roles of humor and sense of humor in responses to stressors. *Humor - International Journal of Humor Research*, *12*(2), pp.177-193.

Cann, A., Norman, M.A., Welbourne, J.L. and Calhoun, L.G., 2008. Attachment styles, conflict styles and humour styles: Interrelationships and associations with relationship satisfaction. *European journal of personality*, *22*(2), pp.131-146.

Caplan, J.P. and Stern, T.A., 2008. Mnemonics in a Mnutshell: 32 Aids to Psychiatric Diagnosis; Clever, Irreverent, or Amusing, a Mnemonic You Remember Is a Lifelong Learning Tool. *Current Psychiatry*, *7*(10), p.27.

Carlson, K.A., 2011. The impact of humor on memory: Is the humor effect about humor?. *Humor - International Journal of Humor Research*, 24(1), pp. 21-41.

Carlson, P. and Peterson, R.L., 1995. What Is Humor and Why Is It Important?. *Reclaiming Children and Youth: Journal of Emotional and Behavioral Problems*, *4*(3), pp.6-12.

Carlsson, K., Petrovic, P., Skare, S., Petersson, K.M. and Ingvar, M., 2000. Tickling expectations: neural processing in anticipation of a sensory stimulus. *Journal of cognitive neuroscience*, *12*(4), pp.691-703.

Carney, R.N. and Levin, J.R., 2003. Promoting higher-order learning benefits by building lower-order mnemonic connections. *Applied Cognitive Psychology*, *17*(5), pp.563-575.

Caron, J.E., 2002. From ethology to aesthetics: Evolution as a theoretical paradigm for research on laughter, humor, and other comic phenomena. *Humor - International Journal of Humor Research*, *15*(3), pp.245-282.

Carpenter, M. and Call, J., 2013. How joint is the joint attention of apes and human infants. *Agency and joint attention*, pp.49-61.

Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C. and Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, *100*(9), pp.5497-5502.

Carruthers, P., 2006. *The architecture of the mind*. Oxford, Oxford University Press.

Carruthers, P. and Chamberlain, A. eds., 2000. *Evolution and the human mind: Modularity, language and meta-cognition*. Cambridge, Cambridge University Press.

Carter, A.S., Garrity-Rokous, F.E., Chazan-Cohen, R., Little, C. and Briggs-Gowan, M.J., 2001. Maternal depression and comorbidity: predicting early parenting, attachment security, and toddler social-emotional problems and competencies. *Journal of the American Academy of Child & Adolescent Psychiatry*, *40*(1), pp.18-26.

Carter, C.S., 1998. Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology*, *23*(8), pp.779-818.

Carter, C.S., 2014. Oxytocin pathways and the evolution of human behavior. *Annual review of psychology*, *65*, pp.17-39.

Catts, H.W., 1991. Facilitating phonological awareness: Role of speech-language pathologists. *Language, Speech, and Hearing Services in Schools*, *22*(4), pp.196-203.

Cha, M.Y. and Hong, H.S., 2015. Effect and Path Analysis of Laughter Therapy on Serotonin, Depression and Quality of Life in Middle-aged Women. *Journal of Korean Academy of Nursing*, *45*(2).

Chan, T.C., Harrigan, R.A., Ufberg, J. and Vilke, G.M., 2008. Mandibular reduction. *The Journal of emergency medicine*, *34*(4), pp.435-440.

Chanda, M.L. and Levitin, D.J., 2013. The neurochemistry of music. *Trends in cognitive sciences*, *17*(4), pp.179-193.

Chang, D., Dooley, L. and Tuovinen, J.E., 2002, July. Gestalt theory in visual screen design: a new look at an old subject. In *Proceedings of the Seventh world conference on computers in education conference on Computers in education: Australian topics-Volume 8* (pp. 5-12). Australian Computer Society, Inc..

Chapais, B., 2013. Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(2), pp.52-65.

Chapman, A.J., 1973. Social facilitation of laughter in children. *Journal of Experimental Social Psychology*, *9*(6), pp.528-541.

Chapman, A.J., 1983. Humor and laughter in social interaction and some implications for humor research. *Handbook of humor research*, *1*, pp.135-157.

Charman, T., Baron-Cohen, S., Swettenham, J., Baird, G., Cox, A. and Drew, A., 2000. Testing joint attention, imitation, and play as infancy precursors to language and theory of mind. *Cognitive development*, *15*(4), pp.481-498.

Chase, P.G. and Dibble, H.L., 1987. Middle Paleolithic symbolism: a review of current evidence and interpretations. *Journal of anthropological archaeology*, *6*(3), pp.263-296.

Chauvin, C., 2017. Callbacks in Stand-Up Comedy: Constructing Cohesion at the Macro Level Within a Specific Genre. In *Contrastive Analysis of Discourse-pragmatic Aspects of Linguistic Genres* (pp. 165-185). New York, Springer International Publishing.

Chen C, Burton M, Greenberger E, et al. 1999. Population migration and the variation of dopamine D4 receptor (DRD4) allele frequencies around the globe. *Evol Hum Behav 20*, pp. 309–324.

Chittka, L., Skorupski, P. and Raine, N.E., 2009. Speed–accuracy tradeoffs in animal decision making. *Trends in ecology & evolution*, *24*(7), pp.400-407.

Chomsky, N., 1986. *Knowledge of language: Its nature, origin, and use*. New York, Praeger.

Chomsky, N., 1988. *Language and problems of knowledge: The Managua lectures* (Vol. 16). Cambridge, Ma., MIT press.

Chomsky, N., 1999. *Derivation by phase* (No. 18). Cambridge, Ma., MIT, Department of Linguistics.

Chomsky, N., 2005. Three factors in language design. *Linguistic inquiry*, *36*(1), pp.1-22.

Chomsky, N., 2014. *The minimalist program*. Cambridge, Ma., MIT Press.

Chow, G.V., Desai, D., Spragg, D.D. and Zakaria, S., 2012. Laughter-Induced Left Bundle Branch Block. *Journal of cardiovascular electrophysiology*, *23*(10), pp.1136-1138.

Chung, H.J., 2011. The effect of laughter therapy on infertility stress and anxiety of women receiving in vitro fertilization. *Fertility and Sterility*, *96*(3), pp.S195-S196.

Chung, H. and Zhao, X., 2003. Humour effect on memory and attitude: moderating role of product involvement. *International Journal of Advertising*, *22*(1), pp.117-144.

Clark, A., Seidler, A. and Miller, M., 2001. Inverse association between sense of humor and coronary heart disease. *International journal of cardiology*, *80*(1), pp.87-88.

Clay, Z. and Zuberbühler, K., 2009. Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*(6), pp.1387-1396.

Clayton, M., 2009. The social and personal functions of music in cross-cultural perspective. *The Oxford handbook of music psychology*, pp.35-44.

Cobb, S., 1976. Social support as a moderator of life stress. *Psychosomatic medicine*, *38*(5), pp.300-314.

Cohen, A., 2002. *Self consciousness: An alternative anthropology of identity*. Florence Kentucky, Routledge.

Collinson, D.L., 1988. 'Engineering humour': masculinity, joking and conflict in shop-floor relations. *Organization Studies*, *9*(2), pp.181-199.

Colom, R., Juan-Espinosa, M., Abad, F. and Garcia, L.F., 2000. Negligible sex differences in general intelligence. *Intelligence*, *28*(1), pp.57-68.

Coppinger, R., Glendinning, J., Torop, E., Matthay, C., Sutherland, M. and Smith, C., 1987, Degree of Behavioral Neoteny Differentiates Canid Polymorphs. *Ethology, 75*, 89–108.

Corballis, M., 1999. The Gestural Origins of Language - Human language may have evolved from manual gestures, which survive today as a" behavioral fossil" coupled to speech. *American Scientist*, *87*(2), pp.138-146.

Corballis, M.C., 2008. The gestural origins of language. In *The Origins of Language* (pp. 11-23). Tokyo, Springer.

Corballis, M.C., 2014. *The recursive mind: The origins of human language, thought, and civilization*. Oxford, Princeton University Press.

Corbin, M.R., 2007. The Importance of Play. *The ITB Journal*, *8*(2), p.6.

Cori, V., Canestrari, C. and Bianchi, I., 2016. The Perception of Contrariety and the Processing of Verbal Irony. *Gestalt Theory*, *38*(2/3).

Coser, R.L., 1959. Some social functions of laughter: A study of humor in a hospital setting. *Human relations*, *12*(2), pp.171-182.

Cosmides, L. and Tooby, J., 1994. Beyond intuition and instinct blindness: Toward an evolutionarily rigorous cognitive science. *Cognition*, *50*(1), pp.41-77.

Cosmides, L. and Tooby, J., 1994. Origins of domain-specificity: The evolution of functional organization. *Mapping the mind: Domain-specificity in cognition and culture*, pp.85-116.

Coulson, S., 2001. What's so funny: conceptual blending in humorous examples. *The poetics of cognition: studies of cognitive linguistics and the verbal arts*.

Coulson, S., 2005. Extemporaneous blending: Conceptual integration in humorous discourse from talk radio. *Style*, *39*(2), pp.107-121.

Craik, K.H., Lampert, M.D. and Nelson, A.J., 1996. Sense of humor and styles of everyday humorous conduct. *Humor-International Journal of Humor Research*, *9*(3-4), pp.273-302.

Craik, K.J.W., 1967. *The nature of explanation* (Vol. 445). CUP Archive.

Cramer, P., 1972. A developmental study of errors in memory. *Developmental Psychology*, *7*(2), p.204.

Crespi, B.J., 2004. Vicious circles: positive feedback in major evolutionary and ecological transitions. *Trends in Ecology & Evolution*, *19*(12), pp.627-633.

Crews, D.E., 2003. *Human senescence: Evolutionary and biocultural perspectives* (Vol. 36). Cambridge, Cambridge University Press.

Critchley, S., 2011. *On humour*. Kentucky, Routledge.

Črnčec, R., Wilson, S.J. and Prior, M., 2006. The cognitive and academic benefits of music to children: Facts and fiction. *Educational Psychology*, *26*(4), pp.579-594.

Crook, J., 1987. The nature of conscious awareness. In Blakemore, C. and Greenfield, S.A.,eds., *Mindwaves: Thoughts on intelligence, identity, and consciousness*. Blackwell Publishing pp.383-402.

Csikszentmihalyi, M., 1996. *Flow and the psychology of discovery and invention*. New York: Harper Collins.

Curcó, C., 1995. Some observations on the pragmatics of humorous interpretations: a relevance theoretic approach. *Working Papers in Linguistics*, *7*, pp.27-47.

Curtis, G., 2007. *The cave painters: Probing the mysteries of the world's first artists*. New York, Knopf.

D'Alfonso, A., Iovenitti, P., Casacchia, M. and Carta, G., 2002. Disturbances of humour in postpartum: our experience. *Clinical and experimental obstetrics & gynecology*, *29*(3), pp.207-211.

D'Azevedo, W.L., 1958. A structural approach to esthetics: toward a definition of art in anthropology. *American Anthropologist*, *60*(4), pp.702-714.

Dalmonte, R., 1995. Towards a semiology of humour in music. *International Review of the Aesthetics and Sociology of Music*, pp.167-187.

Damon, W. and Hart, D., 1982. The development of self-understanding from infancy through adolescence. *Child development*, pp.841-864.

Dart, R.A., 1974. The waterworn australopithecine pebble of many faces from Makapansgat. *South African Journal of Science*, *70*(6), p.167.

Darwin, C., 1965. *The expression of the emotions in man and animals* (Vol. 526). Chicago, University of Chicago Press.

David, B., Geneste, J.M., Petchey, F., Delannoy, J.J., Barker, B. and Eccleston, M., 2013. How old are Australia's pictographs? A review of rock art dating. *Journal of Archaeological Science*, *40*(1), pp.3-10.

Davidheiser, M., 2003. Joking Kinship and Conflict Management: An African Perspective on Dispute Mediation. In *American Anthropological Association Meetings in Chicago, April*.

Davies, C., 1990. *Ethnic humor around the world: A comparative analysis.* Bloomington, IN. Indiana University Press.

Davies, C., 2007. Humour and protest: Jokes under Communism. *International Review of Social History*, *52*(S15), pp.291-305.

Davies, S., 2010. Why art is not a spandrel. *The British Journal of Aesthetics*, *50*(4), pp.333-341.

Davila-Ross, M., Allcock, B., Thomas, C. and Bard, K.A., 2011. Aping expressions? Chimpanzees produce distinct laugh types when responding to laughter of others. *Emotion*, *11*(5), p.1013.

Davila-Ross, M., Jesus, G., Osborne, J. and Bard, K.A., 2015. Chimpanzees (Pan troglodytes) produce the same types of 'laugh faces' when they emit laughter and when they are silent. *PloS one*, *10*(6), p.e0127337.

Davison, J., 2013. *Clown: Readings in theatre practice*. London, Palgrave Macmillan.

Dawkins, R., 2016. *The selfish gene*. Oxford, Oxford University Press.

Dawson, G., Toth, K., Abbott, R., Osterling, J., Munson, J., Estes, A. and Liaw, J., 2004. Early social attention impairments in autism: social orienting, joint attention, and attention to distress. *Developmental psychology*, *40*(2), p.271.

Day, R.L., Coe, R.L., Kendal, J.R. and Laland, K.N., 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, *65*(3), pp.559-571.

De Boer, B., 2005. Evolution of speech and its acquisition. *Adaptive Behavior*, *13*(4), pp.281-292.

De Castro, J.M.B., Martinón-Torres, M., Prado, L., Gómez-Robles, A., Rosell, J., López-Polín, L., Arsuaga, J.L. and Carbonell, E., 2010. New immature hominin fossil from European Lower Pleistocene shows the earliest evidence of a modern human dental development pattern. *Proceedings of the National Academy of Sciences*, *107*(26), pp.11739-11744.

De Groot, A.D., 1978. *Thought and choice in chess* (Vol. 4). New York, Walter de Gruyter GmbH & Co KG.

De Rivera, J., 1992. Emotional climate: Social structure and emotional dynamics. In *A preliminary draft of this chapter was discussed at a workshop on emotional climate sponsored by the Clark European Center in Luxembourg on Jul 12–14, 1991.*. John Wiley & Sons.

De Waal, F.B., 1988. The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour*, *106*(3), pp.183-251.

De Waal, F.B. and Luttrell, L.M., 1985. The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *American Journal of Primatology*, *9*(2), pp.73-85.

De Waal, F.B., 1995. Bonobo sex and society. *Scientific American*, *272*(3), pp.82-88.

Deacon, T., 1997. *The Symbolic Species: The co-evolution of language and the human brain*. London, W.W.Norton and Company.

Deacon, T., 2006. The aesthetic faculty. *The artful mind: Cognitive science and the riddle of human creativity*, pp.21-53.

Deacon, T., 2010. A role for relaxed selection in the evolution of the language capacity. *Proceedings of the National Academy of Sciences*, *107*(Supplement 2), pp.9000-9006.

Deaner, S.L. and McConatha, J.T., 1993. The relation of humor to depression and personality. *Psychological Reports*, *72*(3), pp.755-763.

Decety, J. and Sommerville, J.A., 2003. Shared representations between self and other: a social cognitive neuroscience view. *Trends in cognitive sciences*, *7*(12), pp.527-533.

Dediu, D. and Levinson, S.C., 2013. On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences. *Frontiers in psychology*, *4*, p.397.

Deleuze, G., 1994. *Difference and repetition*. New York, Columbia University Press.

DeLouize, A.M., Coolidge, F.L. and Wynn, T., 2017. Dopaminergic systems expansion and the advent of Homo erectus. *Quaternary International*, *427*, pp.245-252.

Demetriou, A. and Kazi, S., 2013. *Unity and modularity in the mind and self: Studies on the relationships between self-awareness, personality, and intellectual development from childhood to adolescence*. New York, Routledge.

Derks, P., Bogart, E. and Gillikin, L., 1991. Neuroelectrical activity and humor. In *9th International Conference on Humour and Laughter at Brock University, St. Catherines, Canada*.

Descartes, R., 1989. *Passions of the soul*. Indianapolis, Hackett Publishing.

Devereux, P.G., Heffner, K.L., Ong, A.D. and van Dulmen, M.H.M., 2007. Psychophysiological approaches to the study of laughter: toward an integration with positive psychology. In *Ong, Van Dulmen eds., Oxford handbook of methods in positive psychology*, *13*. Oxford, Oxford University Press.

DeYoung, C. G., 2006. Higher-order factors of the Big Five in a multi-informant sample. *Journal of Personality and Social Psychology*, 91, 1138 –1151.

Dezecache, G. and Dunbar, R.I., 2012. Sharing the joke: the size of natural laughter groups. *Evolution and Human Behavior*, *33*(6), pp.775-779.

Di Carlo, Christopher W.. 2010. *How Problem Solving and Neurotransmission in the Upper Paleolithic led to The Emergence and Maintenance of Memetic Equilibrium in Contemporary World Religions*. Journal of Consciousness Exploration & Research| June 2010 | Vol. 1 | Issue 4 | Page 410-428

DiPietro, J.A., 1981. Rough and tumble play: A function of gender. *Developmental psychology*, *17*(1), p.50.

Dickins, T.E. and Dickins, D.W., 2001. Symbols, stimulus equivalence and the origins of language. *Behavior and Philosophy*, pp.221-244.

Dienstbier, R.A., 1995. The impact of humor on energy, tension, task choices, and attributions: Exploring hypotheses from toughness theory. *Faculty Publications, Department of Psychology*, p.111.

Digman, J. M., 1997. Higher-order factors of the Big Five. *Journal of Personality and Social Psychology*, 73, 1246 – 1256.

Dijksterhuis, A., Bargh, J.A. and Miedema, J., 2000. Of men and mackerels: Attention, subjective experience, and automatic social behavior. *The message within: The role of subjective experience in social cognition and behavior*, pp.37-51.

Dillon, K.M., Minchoff, B. and Baker, K.H., 1986. Positive emotional states and enhancement of the immune system. *The International Journal of Psychiatry in Medicine*, *15*(1), pp.13-18.

Diogo, R. and Wood, B., 2011. Soft-tissue anatomy of the primates: phylogenetic analyses based on the muscles of the head, neck, pectoral region and upper limb, with notes on the evolution of these muscles. *Journal of anatomy*, *219*(3), pp.273-359.

Dissanayake, E., 2001. Aesthetic incunabula. *Philosophy and Literature*, *25*(2), pp.335-346.

Dissanayake, E., 2001(2). Becoming homo aestheticus: Sources of aesthetic imagination in mother-infant interactions. *Substance*, *30*(1), pp.85-103.

Dissanayake, E., 2004. Motherese is but one part of a ritualized, multimodal, temporally organized, affiliative interaction. *Behavioral and Brain Sciences*, *27*(4), pp.512-513.

Dissanayake, E., 2008. The arts after Darwin: Does art have an origin and adaptive function. *World art studies: Exploring concepts and approaches*, pp.241-263.

Dissanayake, E., 2009. Root, leaf, blossom, or bole: Concerning the origin and adaptive function of music. *Communicative musicality: Exploring the basis of human companionship*, pp.17-30.

Dissanayake, E., 2017. Ethology, Interpersonal Neurobiology, and Play: Insights into the Evolutionary Origin of the Arts. *American Journal of Play*, *9*(2), p.143.

Dodge, E. and Lakoff, G., 2005. Image schemas: From linguistic analysis to neural grounding. *From perception to meaning: Image schemas in cognitive linguistics*, pp.57-91.

Donald, M., 1991. *Origins of the modern mind: Three stages in the evolution of culture and cognition*. Cumbreland, Harvard University Press.

Donald, M., 2001. *A mind so rare: The evolution of human consciousness*. Scranton, W.W. Norton & Company.

Donald, M., 2006. Art and cognitive evolution. *The artful mind: Cognitive science and the riddle of human creativity*, pp.3-200.

Double, O., 1991. *An approach to traditions of British stand-up comedy* (Doctoral dissertation, University of Sheffield).

Double, O., 2013. *Getting the joke: The inner workings of stand-up comedy*. London, Methuen.

Double, O., 2014. *Stand Up: On Being a Comedian*. London, Methuen.

Douglas, M., 2002. *Implicit meanings*. London, Routledge.

Duchenne, G.B., 1990. *The mechanism of human facial expression*. Cambridge, Cambridge University Press.

Duckworth, G.E., 2015. *Nature of Roman comedy: A study in popular entertainment*. Princeton, Princeton University Press.

Dunbar, R.I., 1993. Coevolution of neocortical size, group size and language in humans. *Behavioral and brain sciences*, *16*(4), pp.681-694.

Dunbar, R.I., 1998(a). The social brain hypothesis. *Brain*, *9*(10), pp.178-190.

Dunbar R.I., 1998(b). *Grooming, Gossip, and The Evolution of Language.* Cambridge, Ma, Harvard University Press.

Dunbar, R.I., 2003. The social brain: mind, language, and society in evolutionary perspective. *Annual Review of Anthropology*, *32*(1), pp.163-181.

Dunbar, R.I., 2004. Language, Music, and Laughter in Evolutionary Perspective. *Evolution of communication systems*, p.257.

Dunbar, R.I., 2009. The social brain hypothesis and its implications for social evolution. *Annals of human biology*, *36*(5), pp.562-572.

Dunbar, R.I., 2012. Bridging the bonding gap: the transition from primates to humans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1597), pp.1837-1846.

Dunbar, R.I., 2017. Group size, vocal grooming and the origins of language. *Psychonomic bulletin & review*, *24*(1), pp.209-212.

Dunbar, R.I., Baron, R., Frangou, A., Pearce, E., van Leeuwin, E.J., Stow, J., Partridge, G., MacDonald, I., Barra, V. and Van Vugt, M., 2011. Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society of London B: Biological Sciences*, p.rspb20111373.

Dunbar, R.I., Launay, J. and Curry, O., 2016. The complexity of jokes is limited by cognitive constraints on mentalizing. *Human Nature*, *27*(2), pp.130-140.

Duncan, W.J., 1985. The superiority theory of humor at work: Joking relationships as indicators of formal and informal status patterns in small, task-oriented groups. *Small Group Behavior*, *16*(4), pp.556-564.

Dundes, A., 1975. Slurs International: Folk Comparisons of Ethnicity and National Character. In *Southern Folklore Quarterly 39, pp. 15-38.*

Dutton, D., 2003. Aesthetics and evolutionary psychology. *The Oxford handbook for aesthetics*, ed. Levinson, J.. Oxford, Oxford University Press, pp.693-705.

Dynel, M., 2011. Blending the incongruity-resolution model and the conceptual integration theory: The case of blends in pictorial advertising. *International Review of Pragmatics*, *3*(1), pp.59-83.

Eastman, M., 1921. *The sense of humor*. New York, C. Scribner and Sons.

Ebstein, R.P., Novick, O., Umansky, R., Priel, B., Osher, Y., Blaine, D., Bennett, E.R., Nemanov, L., Katz, M. and Belmaker, R.H., 1996. Dopamine D4 receptor (D4DR) exon III polymorphism associated with the human personality trait of novelty seeking. *Nature genetics*, *12*(1), pp.78-80.

Eigsti, I.M., de Marchena, A.B., Schuh, J.M. and Kelley, E., 2011. Language acquisition in autism spectrum disorders: A developmental review. *Research in Autism Spectrum Disorders*, *5*(2), pp.681-691.

Eisenberg, L., 1995. The social construction of the human brain. *American Journal of Psychiatry*, *152*(11), pp.1563-1575.

Eisenhower, D., Mathiowetz, N.A. and Morganstein, D., 1991. Recall error: Sources and bias reduction techniques. *Measurement errors in surveys*, pp.125-144.

Ekman, P., 1993. Facial expression and emotion. *American psychologist*, *48*(4), p.384.

Ekman, P., and Friesen, W.V., 1982. *Felt, false and miserable smiles*. Journal of Nonverbal Behavior 6: 238–252.

Ekman, P., Friesen, W.V. and O'sullivan, M., 1988. Smiles when lying. *Journal of personality and social psychology*, *54*(3), p.414.

Ekman, P., O'Sullivan, M., Friesen, W.V. and Scherer, K.R., 1991. Invited article: Face, voice, and body in detecting deceit. *Journal of nonverbal behavior*, *15*(2), pp.125-135.

Elsenbruch, S., Benson, S., Rücke, M., Rose, M., Dudenhausen, J., Pincus-Knackstedt, M.K., Klapp, B.F. and Arck, P.C., 2006. Social support during pregnancy: effects on maternal depressive symptoms, smoking and pregnancy outcome. *Human reproduction*, *22*(3), pp.869-877.

Emde, R.N. and Koenig, K.L., 1969. Neonatal smiling and rapid eye movement states. *Journal of the American Academy of Child Psychiatry*, *8*(1), pp.57-67.

Enard, W., 2011. FOXP2 and the role of cortico-basal ganglia circuits in speech and language evolution. *Current opinion in neurobiology*, *21*(3), pp.415-424.

Enard, W., Przeworski, M., Fisher, S.E., Lai, C.S., Wiebe, V., Kitano, T., Monaco, A.P. and Pääbo, S., 2002. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, *418*(6900), p.869.

Endler, J.A., 2012. Bowerbirds, art and aesthetics: Are bowerbirds artists and do they have an aesthetic sense?. *Communicative & integrative biology*, *5*(3), pp.281-283.

Endress, A.D., Carden, S., Versace, E. and Hauser, M.D., 2010. The apes' edge: positional learning in chimpanzees and humans. *Animal cognition*, *13*(3), pp.483-495.

Engler, A.C., Hadash, A., Shehadeh, N. and Pillar, G., 2012. Breastfeeding may improve nocturnal sleep and reduce infantile colic: potential role of breast milk melatonin. *European journal of pediatrics*, *171*(4), pp.729-732.

Esseily, R., Rat-Fischer, L., Somogyi, E., O'Regan, K.J. and Fagard, J., 2016. Humour production may enhance observational learning of a new tool-use action in 18-month-old infants. *Cognition and Emotion*, *30*(4), pp.817-825.

Everts, E., 2003. Identifying a particular family humor style: A sociolinguistic discourse analysis. *Humor – International Journal of Humour Studies*, *16*(4), pp.369-412.

Eysenck, H.J., 1942. The appreciation of humour: an experimental and theoretical study 1. *British Journal of Psychology. General Section*, *32*(4), pp.295-309.

Falk, D., 2004. Prelinguistic evolution in early hominins: Whence motherese?. *Behavioral and Brain Sciences*, *27*(4), pp.491-503.

Falkenberg, I., Buchkremer, G., Bartels, M. and Wild, B., 2011. Implementation of a manual-based training of humor abilities in patients with depression: A pilot study. *Psychiatry Research*, *186*(2), pp.454-457.

Fantz, R.L., 1964. Visual experience in infants: Decreased attention to familiar patterns relative to novel ones. *Science*, *146*(3644), pp.668-670.

Fasel, B. and Luettin, J., 2003. Automatic facial expression analysis: a survey. *Pattern recognition*, *36*(1), pp.259-275.

Fauconnier, G. and Turner, M., 1996. Blending as a central process of grammar. In *Conceptual structure, discourse, and language, ed. Goldberg, A*. USA, Center for the Study of Language and Information, p.130.

Fauconnier, G. and Turner, M., 1998. Conceptual integration networks. *Cognitive science*, *22*(2), pp.133-187.

Fauconnier, G. and Turner, M., 2003. Conceptual blending, form and meaning. *Recherches en communication*, *19*(19), pp.57-86.

Fauconnier, G. and Turner, M., 2006. The origin of language as a product of the evolution of modern cognition. In *Origin and Evolution of Languages: Approaches, Models, Paradigms, Bernard Laks, ed., Equinox. March 2008.*

Fauconnier, G. and Turner, M., 2008. *The way we think: Conceptual blending and the mind's hidden complexities*. New York, Basic Books.

Fecteau, J.H. and Munoz, D.P., 2006. Salience, relevance, and firing: a priority map for target selection. *Trends in cognitive sciences*, *10*(8), pp.382-390.

Fedurek, P. and Slocombe, K.E., 2011. Primate vocal communication: a useful tool for understanding human speech and language evolution?. *Human Biology*, *83*(2), pp.153-173.

Feinberg, T.E. and Mallatt, J., 2016. The nature of primary consciousness. A new synthesis. *Consciousness and cognition*, *43*, pp.113-127.

Feingold, A., 1992. Gender differences in mate selection preferences: A test of the parental investment model. *Psychological bulletin*, *112*(1), p.125.

Feingold, A. and Mazzella, R., 1991. Psychometric intelligence and verbal humor ability. *Personality and Individual Differences*, *12*(5), pp.427-435.

Ferguson, M.A. and Ford, T.E., 2008. Disparagement humor: A theoretical and empirical review of psychoanalytic, superiority, and social identity theories. *Humor-International Journal of Humor Research*, *21*(3), pp.283-312.

Ferner, R.E. and Aronson, J.K., 2013. Laughter and MIRTH (Methodical Investigation of Risibility, Therapeutic and Harmful): narrative synthesis. *BMJ*, *347*, p.f7274.

Field, T.M., Woodson, R., Cohen, D., Greenberg, R., Garcia, R. and Collins, K., 1983. Discrimination and imitation of facial expressions by term and preterm neonates. *Infant Behavior and Development*, *6*(4), pp.485-489.

Fine, G.A. and Soucey, M.D., 2005. Joking cultures: Humor themes as social regulation in group life. *Humor-International Journal of Humor Research*, *18*(1), pp.1-22.

Fink, J.S. and Smith, G.P., 1979. Decreased locomotor and investigatory exploration after denervation of catecholamine terminal fields in the forebrain of rats. *Journal of Comparative and Physiological Psychology*, *93*(1), p.34.

Fisher, M.S., 1997. The effect of humor on learning in a planetarium. *Science Education*, *81*(6), pp.703-713.

Fisher, R.A., 1915. The evolution of sexual preference. *The Eugenics Review*, *7*(3), p.184.

Fisher, S.E., Vargha-Khadem, F., Watkins, K.E., Monaco, A.P. and Pembrey, M.E., 1998. Localisation of a gene implicated in a severe speech and language disorder. *Nature genetics*, *18*(2), pp.168-170.

Fitch, W.T., 2000. The evolution of speech: a comparative review. *Trends in cognitive sciences*, *4*(7), pp.258-267.

Fitch, W.T., 2005. The evolution of music in comparative perspective. *Annals of the New York Academy of Sciences*, *1060*(1), pp.29-49.

Fitch, W.T., 2006. The biology and evolution of music: A comparative perspective. *Cognition*, *100*(1), pp.173-215.

Fitch, W.T., Hauser, M.D. and Chomsky, N., 2005. The evolution of the language faculty: clarifications and implications. *Cognition*, *97*(2), pp.179-210.

Flamson, T. and Barrett, H.C., 2008. The encryption theory of humor: A knowledge-based mechanism of honest signaling. *Journal of Evolutionary Psychology*, *6*(4), pp.261-281.

Flamson, T., Bryant, G.A. and Barrett, H.C., 2011. Prosody in spontaneous humor: Evidence for encryption. *Pragmatics & Cognition*, *19*(2), pp.248-267.

Flinn, M.V. and Ward, C.V., 2005. Ontogeny and evolution of the social child. In *Origins of the social mind: Evolutionary psychology and child development, ed. BJ Ellis & DF Bjorklund*. New York, The Guilford Press, pp.19-44.

Flinn, M.V., Geary, D.C. and Ward, C.V., 2005. Ecological dominance, social competition, and coalitionary arms races: Why humans evolved extraordinary intelligence. *Evolution and Human Behavior*, *26*(1), pp.10-46.

Flugel, J.C., 1954. Humor and laughter. *Handbook of social psychology*, *2. Eds. Fiske, s., Gilbert, D., and Lindzey, G.*. New York, Wiley, pp.709-734.

Flusberg, S.J. and McClelland, J.L., 2014. Connectionism and the emergence of mind. *The Oxford handbook of cognitive science*, *1, ed. Chipman, S*. Oxford, Oxford University Press.

Fodor, J., 1983. *The modularity of mind: An essay on faculty psychology*. Cambridge, Ma., MIT press.

Fodor, J., 1985. Precis of the modularity of mind. *Behavioral and brain sciences*, *8*(1), pp.1-5.

Foer, J., 2011. *Moonwalking with Einstein: The art and science of remembering everything*. New York, Penguin.

Fogel, A., Nwokah, E., Dedo, J.Y., Messinger, D., Dickson, K.L., Matusov, E. and Holt, S.A., 1992. Social process theory of emotion: A dynamic systems approach. *Social Development*, *1*(2), pp.122-142.

Foley, R.A. and Lee, P.C., 1989. Finite social space, evolutionary pathways, and reconstructing hominid behavior. *Science*, *243*(4893), pp.901-906.

Fonagy, P., Gergely, G. and Target, M., 2007. The parent–infant dyad and the construction of the subjective self. *Journal of child psychology and psychiatry*, *48*(3-4), pp.288-328.

Foot, H.C. and Chapman, A.J., 1976. The social responsiveness of young children in humorous situations. In *Humor and laughter: Theory, research, and applications,* ed. Chapman, A.J.. New York, Wiley and Sons, pp.187-214.

Forabosco, G., 2008. Is the concept of incongruity still a useful construct for the advancement of humor research?. *Lodz Papers in Pragmatics*, *4*(1), pp.45-62.

Foster, M.L., 1994. Language as Analogic Strategy: Suggestions for Evolutionary Research. In *Studies in Language Origins, Volume 3*, eds., Wind, Abraham and Jonker. Philadelphia, John Benjamins Publishing.

Fouts, R.S., Chown, B. and Goodin, L., 1976. Transfer of signed responses in American Sign Language from vocal English stimuli to physical object stimuli by a chimpanzee (Pan). *Learning and Motivation*, *7*(3), pp.458-475.

Fox, M.W., 1978: *The Dog: Its domestication and behavior.* New York and London, Garland STPM Press.

Fox, M.W. and Fox, M.W., 1974. *Concepts in ethology: Animal and human behavior*. Minneapolis, Minn.: University of Minnesota Press.

Francis, J.J., O'Connor, D. and Curran, J., 2012. Theories of behaviour change synthesised into a set of theoretical groupings: introducing a thematic series on the theoretical domains framework. *Implementation Science*, *7*(1), p.35.

Francis, L.E., 1994. Laughter, the best mediation: Humor as emotion management in interaction. *Symbolic Interaction*, *17*(2), pp.147-163.

Frank, S.L., Bod, R. and Christiansen, M.H., 2012. How hierarchical is language use?. *Proceedings of the Royal Society of London B: Biological Sciences*, p.rspb20121741.

Frankenhuis, W. and Ploeger, A., 2007. Evolutionary psychology versus Fodor: Arguments for and against the massive modularity hypothesis. *Philosophical Psychology*, *20*(6), pp.687-710.

Frankish, K., 2016. Illusionism as a theory of consciousness. *Journal of Consciousness Studies*, *23*(11-12), pp.11-39.

Franklin, T.B., Russig, H., Weiss, I.C., Gräff, J., Linder, N., Michalon, A., Vizi, S. and Mansuy, I.M., 2010. Epigenetic transmission of the impact of early stress across generations. *Biological psychiatry*, *68*(5), pp.408-415.

Frecknall, P., 1994. Good humor: A qualitative study of the uses of humor in everyday life. *Psychology: A Journal of Human Behavior*. *31*(1), 12-21.

Fredrickson, B.L., 1998. What good are positive emotions?. *Review of general psychology*, *2*(3), p.300.

Fredrickson, B.L., 2001. The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American psychologist*, *56*(3), p.218.

Fredrickson, B.L. and Joiner, T., 2002. Positive emotions trigger upward spirals toward emotional well-being. *Psychological science*, *13*(2), pp.172-175.

Freedman, J., 1977. Joking, affinity and the exchange of ritual services among the Kiga of Northern Rwanda: an essay on joking relationship theory. *Man*, pp.154-165.

French, R.M., 2002. The computational modeling of analogy-making. *Trends in cognitive Sciences*, *6*(5), pp.200-205.

Freud, S., 1960. Jokes and their relation to the unconscious. Standard Edition, Vol. 8. *Trans. and ed. J. Strachey.* London, Hogarth Press.

Fridlund, A.J. and Loftis, J.M., 1990. Relations between tickling and humorous laughter: Preliminary support for the Darwin-Hecker hypothesis. *Biological Psychology*, *30*(2), pp.141-150.

Fridlund, A.J., 1991. Sociality of solitary smiling: Potentiation by an implicit audience. *Journal of Personality and Social Psychology*, *60*(2), p.229.

Friedler, S., Glasser, S., Azani, L., Freedman, L.S., Raziel, A., Strassburger, D., Ron-El, R. and Lerner-Geva, L., 2011. The effect of medical clowning on pregnancy rates after in vitro fertilization and embryo transfer. *Fertility and Sterility*, *95*(6), pp.2127-2130.

Fry, A.F. and Hale, S., 1996. Processing speed, working memory, and fluid intelligence: Evidence for a developmental cascade. *Psychological science*, *7*(4), pp.237-241.

Fry, W.F., 1984, June. Learning with humor. In *annual meeting of the International Conference on Humor, Tel Aviv, Israel*.

Fry, W.F., 1994. The biology of humor. *Humor-International Journal of Humor Research*, *7*(2), pp.111-126.

Fry Jr, W.F., 1987. Humor and paradox. *American Behavioral Scientist*, *30*(3), pp.42-71.

Fuster, J.M., 2002. Frontal lobe and cognitive development. *Journal of neurocytology*, *31*(3-5), pp.373-385.

Gaertner, L., Sedikides, C. and Graetz, K., 1999. In search of self-definition: Motivational primacy of the individual self, motivational primacy of the collective self, or contextual primacy?. *Journal of personality and social psychology*, *76*(1), p.5.

Galef, B.G., 1992. The question of animal culture. *Human nature*, *3*(2), pp.157-178.

Gallese, V., 2007. Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), pp.659-669.

Galvan, D., 2006. Joking kinship as a syncretic institution. *Cahiers d'études africaines*, *46*(184), pp.809-834.

Gamble, J., 2001. Humor in apes. *Humor – International Journal of Humor Research*, 14(2), pp. 163-179.

Gao, W., Zhu, H., Giovanello, K.S., Smith, J.K., Shen, D., Gilmore, J.H. and Lin, W., 2009. Evidence on the emergence of the brain's default network from 2-week-old to 2-year-old healthy pediatric subjects. *Proceedings of the National Academy of Sciences*, *106*(16), pp.6790-6795.

Garcia, J.R., MacKillop, J., Aller, E.L., Merriwether, A.M., Wilson, D.S. and Lum, J.K., 2010. Associations between dopamine D4 receptor gene variation with both infidelity and sexual promiscuity. *PLoS One*, *5*(11), p.e14162.

Gardiner, A.H., 1932. *The theory of speech and language.* Oxford, England: Oxford University Press.

Gardner, H., 2011. *Frames of mind: The theory of multiple intelligences*. New York, Basic Books.

Gardner, R.A. and Gardner, B.T., 1969. Teaching sign language to a chimpanzee. *Science*, *165*(3894), pp.664-672.

Gardner, R. A., & Gardner, B. T.,1989. A test of communication. In R. A. Gardner, B. T. Gardner, & T. E. Van Cantfort Eds., *Teaching sign language to chimpanzees*. Albany: State University of New York Press, pp. 181-197.

Gardner, R.A., Gardner, B.T. and Van Cantfort, T.E. eds., 1989. *Teaching sign language to chimpanzees*. New York, Suny Press.

Geertz, C., 1973. *The interpretation of cultures* (Vol. 5019). New York, Basic Books.

Geist, V., 2013. *Life strategies, human evolution, environmental design: toward a biological theory of health*. New York, Springer Science & Business Media.

Gelb, B.D. and Zinkhan, G.M., 1986. Humor and advertising effectiveness after repeated exposures to a radio commercial. *Journal of Advertising*, *15*(2), pp.15-34.

Gerry, D., Unrau, A. and Trainor, L.J., 2012. Active music classes in infancy enhance musical, communicative and social development. *Developmental science*, *15*(3), pp.398-407.

Gervais, M. and Wilson, D.S., 2005. The evolution and functions of laughter and humor: A synthetic approach. *The Quarterly Review of Biology*, *80*(4), pp.395-430.

Ghosh, V.E. and Gilboa, A., 2014. What is a memory schema? A historical perspective on current neuroscience literature. *Neuropsychologia*, *53*, pp.104-114.

Gibson, R., 1994. *Tools, language and cognition in human evolution*. Cambridge, Cambridge University Press.

Gibbs, R. and Van Orden, G., 2010. Adaptive cognition without massive modularity. *Language and Cognition*, *2*(2), pp.149-176.

Gibson, K.R., 1991. Myelination and behavioral development: A comparative perspective on questions of neoteny, altriciality and intelligence. *Brain maturation and cognitive development: Comparative and cross-cultural perspectives*, pp.29-63.

Gibson, K.R. and Petersen, A.C.,1991. *Brain maturation and cognitive development: comparative and cross-cultural perspectives*. Hawthorne, New York, Transaction Publishers.

Gick, M.L. and Holyoak, K.J., 1983. Schema induction and analogical transfer. *Cognitive psychology*, *15*(1), pp.1-38.

Gignac, G.E., Karatamoglou, A., Wee, S. and Palacios, G., 2014. Emotional intelligence as a unique predictor of individual differences in humour styles and humour appreciation. *Personality and Individual Differences*, *56*, pp.34-39.

Gillan, D.J., Premack, D. and Woodruff, G., 1981. Reasoning in the chimpanzee: I. Analogical reasoning. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*(1), p.1.

Gillespie, T., 2014. The relevance of algorithms. *Media technologies: Essays on communication, materiality, and society*, *167*.

Girard, R., 1965. Deceit, desire, and the novel. In *The Novel: An Anthology of Criticism and Theory 1900–2000*, ed. Hale, D.. Malden, Ma., Blackwell Publishing, pp.294-314.

Givón, T.,1998. On the co-evolution of language, mind and brain. *Evolution of communication*, 2, 45-116.

Gleason, J.B., 2005. *The Development Of Language,* 6/e. Boston, Allyn and Bacon.

Glenn, S.A., 1998. " Give an Imitation of Me": Vaudeville Mimics and the Play of the Self. *American Quarterly*, *50*(1), pp.47-76.

Godfrey, L.R. and Sutherland, M.R., 1996. Paradox of peramorphic paedomorphosis: heterochrony and human evolution. *American journal of physical anthropology*, *99*(1), pp.17-42.

Godfrey, L.R., Samonds, K.E., Jungers, W.L. and Sutherland, M.R., 2001. Teeth, brains, and primate life histories. *American Journal of Physical Anthropology*, *114*(3), pp.192-214.

Goffman, E., 1969. *The presentation of self in everyday life.* London, Allen Lane.

Goldberg, G., 1985. Supplementary motor area structure and function: review and hypotheses. *Behavioral and brain Sciences*, *8*(4), pp.567-588.

Goldberg, L.R., 1981. Language and individual differences: The search for universals in personality lexicons. *Review of personality and social psychology*, *2*(1), pp.141-165.

Goldman, S.R., Meyerson, P.M. and Cote, N., 2006. Poetry as a mnemonic prompt in children's stories. *Reading Psychology*, *27*(4), pp.345-376.

Goldstein, J.H., Suls, J.M. and Anthony, S., 1972. Enjoyment of specific types of humor content: Motivation or salience. *The psychology of humor: Theoretical perspectives and empirical issues*, pp.159-171.

Gómez, J.C., 1996. Ostensive behavior in great apes: The role of eye contact. *Reaching into thought: The minds of the great apes*, ed. Russon, A.. Cambridge, Cambridge University Press, pp.131-151.

Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns of Behavior*, Cambridge, Ma., Belknap Press.

Gopnik, A. and Meltzoff, A., 1993. Imitation, cultural learning and the origins of “theory of mind”. *Behavioral and Brain Sciences*, *16*(3), pp.521-523.

Goswami, U. and Brown, A.L., 1990. Melting chocolate and melting snowmen: Analogical reasoning and causal relations. *Cognition*, *35*(1), pp.69-95.

Gould, S.J. and Vrba, E.S., 1982. Exaptation—a missing term in the science of form. *Paleobiology*, *8*(1), pp.4-15.

Gould, S.J., 1977. *Ontogeny and Phylogeny*, Cambridge, MA Belknap Press.

Gould, S.J., 1991. Exaptation: A crucial tool for an evolutionary psychology. *Journal of social issues*, *47*(3), pp.43-65.

Goyal, M.S., Hawrylycz, M., Miller, J.A., Snyder, A.Z. and Raichle, M.E., 2014. Aerobic glycolysis in the human brain is associated with development and neotenous gene expression. *Cell metabolism*, *19*(1), pp.49-57.

Grafen, A., 1990. Sexual selection unhandicapped by the Fisher process. *Journal of theoretical biology*, *144*(4), pp.473-516.

Graziano, W.G., Jensen-Campbell, L.A., Todd, M. and Finch, J.F., 1997. Interpersonal attraction from an evolutionary psychology perspective: Women’s reactions to dominant and prosocial men. *Evolutionary social psychology*, pp.141-167.

Greengross, G., 2014. Male production of humor produced by sexually selected psychological adaptations. In *Evolutionary perspectives on human sexual psychology and behavior* (pp. 173-196). New York, Springer.

Greengross, G., Martin, R.A. and Miller, G., 2012. Personality traits, intelligence, humor styles, and humor production ability of professional stand-up comedians compared to college students. *Psychology of Aesthetics, Creativity, and the Arts*, *6*(1), p.74.

Greengross, G. and Miller, G., 2008. Dissing oneself versus dissing rivals: Effects of status, personality, and sex on the short-term and long-term attractiveness of self-deprecating and other-deprecating humor. *Evolutionary Psychology*, *6*(3), p.147470490800600303.

Greengross, G. and Miller, G., 2011. Humor ability reveals intelligence, predicts mating success, and is higher in males. *Intelligence*, *39*(4), pp.188-192.

Greven, C., Chamorro-Premuzic, T., Arteche, A. and Furnham, A., 2008. A hierarchical integration of dispositional determinants of general health in students: The Big Five, trait emotional intelligence and humour styles. *Personality and Individual differences*, *44*(7), pp.1562-1573.

Griebel U., Oller D., 2008. Evolutionary forces favoring communicative flexibility, in *Evolution of Communicative Flexibility: Complexity, Creativity, and Adaptability in Human and Animal Communication*, eds Oller D. K., Griebel U., editors. Cambridge, Ma., MIT Press.

Groch, A.S., 1974. Joking and appreciation of humor in nursery school children. *Child Development*, pp.1098-1102.

Gruner, C.R., 1978. *Understanding laughter: The workings of wit & humor*. London, Burnham Incorporated Publishers.

Gruner, C.R., 2000. *The game of humor: A comprehensive theory of why we laugh*. New York, Transaction Publishers.

Gundelach, P., 2000. Joking relationships and national identity in Scandinavia. *Acta Sociologica*, *43*(2), pp.113-122.

Gunnery, S.D. and Hall, J.A., 2014. The Duchenne smile and persuasion. *Journal of Nonverbal Behavior*, *38*(2), pp.181-194.

Gvozdover, M.D., 1989. The typology of female figurines of the Kostenki Paleolithic culture. *Soviet Anthropology and Archeology*, *27*(4), pp.32-94.

Haakana, M., 2010. Laughter and smiling: Notes on co-occurrences. *Journal of Pragmatics*, *42*(6), pp.1499-1512.

Hall, G.S. and Allińn, A., 1897. The psychology of tickling, laughing, and the comic. *The American Journal of Psychology*, *9*(1), pp.1-41.

Hamer, D.H., 2002. Genetics of sexual behavior. *Molecular genetics and the human personality*, eds. Benjamin, J., Ebstein, R., Belmaker, R.. Washington, American Psychiatric Association, pp.257-272.

Hamer, D.H. and Copeland, P., 1994. *The science of desire: The search for the gay gene and the biology of behavior*. New York, Simon & Schuster.

Hampes, W.P., 1993. Relation between humor and generativity. *Psychological reports*, *73*(1), pp.131-136.

Hampes, W.P., 1994. Relation between intimacy and the Multidimensional Sense of Humor Scale. *Psychological Reports*, *74*(3_suppl), pp.1360-1362.

Hampes, W.P., 1999. The relationship between humor and trust. *Humor-International Journal of Humor Research*, *12*(3), pp.253-260.

Hampes, W.P., 2001. Relation between humor and empathic concern. *Psychological reports*, *88*(1), pp.241-244.

Hampes, W.P., 2006. Humor and shyness: The relation between humor styles and shyness. *Humor - International Journal of Humor Research, Volume 19, Issue 2,* pp. 179–187.

Hannon, E.E. and Trainor, L.J., 2007. Music acquisition: effects of enculturation and formal training on development. *Trends in cognitive sciences*, *11*(11), pp.466-472.

Hardin, C.D. and Higgins, E.T., 1996. Shared reality: How social verification makes the subjective objective. In *Handbook of motivation and cognition. Handbook of motivation and cognition, Vol. 3. The interpersonal context*, eds., R. M. Sorrentino & E. T. Higgins. New York, Guilford Press, pp. 28-84.

Hare, B., 2017. Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual review of psychology*, *68*, pp.155-186.

Harris, C.R., 2012. Two Forms of Tickle: Knismesis and Gargalesis. In *The Encyclopedia of Human Behaviour,* ed. Ramachandran, V.. New York, Academic Press.

Harris, C.R. and Christenfeld, N., 1997. Humour, tickle, and the Darwin-Hecker hypothesis. *Cognition & Emotion*, *11*(1), pp.103-110.

Harris, D.V., 1970. On the brink of catastrophe. *Quest*, *13*(1), pp.33-40.

Harrison, M., 1998. *The language of theatre*. Manchester, Carcanet Press.

Harrod, J.B., 2014, February. Palaeoart at two million years ago? a review of the evidence. In *Arts* (Vol. 3, No. 1, pp. 135-155). Multidisciplinary Digital Publishing Institute.

Hart, M.T., 2007. Humour and social protest: An introduction. *International Review of Social History*, *52*(S15), pp.1-20.

Hartley, D., 1775. *Hartley's Theory of the Human Mind: On the Principle of the Association of Ideas; with Essays Relating to the Subject of it*. London, J. Johnson.

Hatton, D.C., Harrison-Hohner, J., Coste, S., Dorato, V., Curet, L.B. and McCarron, D.A., 2005. Symptoms of postpartum depression and breastfeeding. *Journal of Human Lactation*, *21*(4), pp.444-449.

Hauck, W.E. and Thomas, J.W., 1972. The relationship of humor to intelligence, creativity, and intentional and incidental learning. *The journal of experimental education*, *40*(4), pp.52-55.

Hauser, M.D., Chomsky, N. and Fitch, W.T., 2002. The faculty of language: what is it, who has it, and how did it evolve?. *Science*, *298*(5598), pp.1569-1579.

Hayashi, K., Hayashi, T., Iwanaga, S., Kawai, K., Ishii, H., Shoji, S.I. and Murakami, K., 2003. Laughter lowered the increase in postprandial blood glucose. *Diabetes care*, *26*(5), pp.1651-1652.

Hayashi, T., Tsujii, S., Iburi, T., Tamanaha, T., Yamagami, K., Ishibashi, R., Hori, M., Sakamoto, S., ISHII, H. and Murakami, K., 2007. Laughter up-regulates the genes related to NK cell activity in diabetes. *Biomedical Research*, *28*(6), pp.281-285.

Hayashi, T., Urayama, O., Hori, M., Sakamoto, S., Nasir, U.M., Iwanaga, S., Hayashi, K., Suzuki, F., Kawai, K. and Murakami, K., 2007. Laughter modulates prorenin receptor gene expression in patients with type 2 diabetes. *Journal of psychosomatic research*, *62*(6), pp.703-706.

Hayashi, T., Urayama, O., Kawai, K., Hayashi, K., Iwanaga, S., Ohta, M., Saito, T. and Murakami, K., 2005. Laughter regulates gene expression in patients with type 2 diabetes. *Psychotherapy and psychosomatics*, *75*(1), pp.62-65.

Hayworth, D., 1928. The social origin and function of laughter. *Psychological Review*, *35*(5), p.367.

Heath, M., 1989. Aristotelian comedy. *The Classical Quarterly*, *39*(2), pp.344-354.

Hebb, D.O., 1955. Drives and the CNS (conceptual nervous system). *Psychological review*, *62*(4), p.243.

Hecht, M.A. and LaFrance, M., 1998. License or obligation to smile: The effect of power and sex on amount and type of smiling. *Personality and Social Psychology Bulletin*, *24*(12), pp.1332-1342.

Hecker, E., 1873. *Die Physiologie und Psychologie des Lachens und des Komischen [The physiology and psychology of laughter and amusement]*. Berlin, F. Dummler.

Hedges, S.B., Marin, J., Suleski, M., Paymer, M. and Kumar, S., 2015. Tree of life reveals clock-like speciation and diversification. *Molecular biology and evolution*, p.msv037.

Hempelmann, C., 2013. *How humour has not evolved.* Huffington Post, https://www.huffingtonpost.com/christian-hempelmann/how-humor-has-not-evolved_b_3692033.html

Hempelmann, C.F., 2007. The laughter of the 1962 Tanganyika 'laughter epidemic'. *Humor – International Journal of Humor Research*, 20(1), pp. 49-71.

Henke, R., 1996. Orality and literacy in the Commedia dell'Arte and the Shakespearean clown. *Oral Tradition*, *11*(2), pp.222-248.

Hennion, A., 2003. Music and mediation: Towards a new sociology of music. In *The cultural study of music: A critical introduction,* ed., Clayton, M.. London, Routledge, pp. 80-91.

Henriksen, G. and Willoch, F., 2007. Imaging of opioid receptors in the central nervous system. *Brain*, *131*(5), pp.1171-1196.

Hensch, T.K., 2005. Critical period plasticity in local cortical circuits. *Nature Reviews Neuroscience*, *6*(11), pp.877-888.

Henshilwood, C.S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A., Mercier, N., Sealy, J.C., Valladas, H., Watts, I. and Wintle, A.G., 2002. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science*, *295*(5558), pp.1278-1280.

Henshilwood, C.S., d'Errico, F., Van Niekerk, K.L., Coquinot, Y., Jacobs, Z., Lauritzen, S.E., Menu, M. and García-Moreno, R., 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science*, *334*(6053), pp.219-222.

Herms, A.D.G., Veit, R., Reisenauer, C., Herms, A., Grodd, W., Enck, P., Stenzl, A. and Birbaumer, N., 2006. Functional imaging of stress urinary incontinence. *Neuroimage*, *29*(1), pp.267-275.

Herrmann, E., Call, J., Hernández-Lloreda, M.V., Hare, B. and Tomasello, M., 2007. Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*(5843), pp.1360-1366.

Hertzler, J.O., 1970. *Laughter: A socio-scientific analysis.* Jericho, N.Y., Exposition Press.

Hessler N.A., Doupe, A.J,. 1999. Social context modulates singing-related neural activity in the songbird forebrain. *Nat Neurosci* 2*:* pp.209–211.

Hewitt, L.E., 1958. Student perceptions of traits desired in themselves as dating and marriage partners. *Marriage and Family Living*, *20*(4), pp.344-349.

Hewstone, M., Rubin, M. and Willis, H., 2002. Intergroup bias. *Annual review of psychology*, *53*(1), pp.575-604.

Heyes, C.M., 1993. Imitation, culture and cognition. *Animal Behaviour*, *46*(5), pp.999-1010.

Heyes, C.M., 1996. Genuine imitation. *Social learning in animals: The roots of culture*, pp.371-389.

Heyes, C.M., 1998. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*(1), pp.101-114.

Heyes, C.M., 2016. Homo imitans? Seven reasons why imitation couldn't possibly be associative. *Phil. Trans. R. Soc. B*, *371*(1686), p.20150069.

Heylighen, F. and Chielens, K., 2009. Evolution of culture, memetics. In *Encyclopedia of complexity and systems science*. New York, Springer, pp. 3205-3220.

Hilgard, E.R., 1980. The trilogy of mind: Cognition, affection, and conation. *Journal of the History of the Behavioral Sciences*, *16*(2), pp.107-117.

Hillis, K., Petit, M. and Jarrett, K., 2012. *Google and the Culture of Search*. London, Routledge.

Hintzman, D.L., 1976. Repetition and memory. In *Psychology of learning and motivation*, *10*, ed. G. Bower. New York, Academic Press, pp.47-91.

Hirschfeld, L.A. and Gelman, S.A. eds., 1994. *Mapping the mind: Domain-specificity in cognition and culture*. Cambridge, Cambridge University Press.

Hixson, M.D., 1998. Ape language research: A review and behavioral perspective. *The Analysis of Verbal Behavior*, *15*(1), pp.17-39.

Ho, S.Y., Phillips, M.J., Cooper, A. and Drummond, A.J., 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Molecular biology and evolution*, *22*(7), pp.1561-1568.

Hobbes, T., 1999. *The Elements of Law, Natural and Politic: Part I, Human Nature, Part II, De Corpore Politico; with Three Lives*. Oxford, Oxford University Press, USA.

Hockett, C.F. and Hockett, C.D., 1960. The origin of speech. *Scientific American*, *203*(3), pp.88-97.

Hodgson, D. 2000a. Art, Perception and Information Processing: An evolutionary Perspective. Rock Art Research17(1), pp. 3–34.

Hodgson, D., 2006. Understanding the origins of paleoart: the neurovisual resonance theory and brain functioning. *Paleoanthropology*, *2006*, pp.54-67.

Hodgson, D., 2008. The visual dynamics of Upper Palaeolithic cave art. *Cambridge Archaeological Journal*, *18*(3), pp.341-353.

Hodgson, D., 2009. Evolution of the visual cortex and the emergence of symmetry in the Acheulean techno-complex. *Comptes Rendus Palevol*, *8*(1), pp.93-97.

Hodgson, D., 2011. The first appearance of symmetry in the human lineage: where perception meets art. *Symmetry*, *3*(1), pp.37-53.

Hoffmann, D., Standish, C., Garcia-Diez, M., Pettitt, P., Milton, J., Zilhao, J., Alcolea-Gonzalez, J., Cantalejo-Duarte, P., Collado, H., D Balbin, R., Lorblanchet, M., Ramos-Munoz, J., Ch. Weniger, G., Pike, A., 2018., U-Th dating of carbonate crusts reveals Neanderthal origin of Iberian cave art. *Science*, 23 Feb 2018 pp. 912-915.

Hofstadter, D.R., 2001. Analogy as the core of cognition. *The analogical mind: Perspectives from cognitive science*, pp.499-538.

Hofstadter, D.R., 2007. *I am a strange loop*. New York, Basic Books.

Hofstadter, D.R. and Sander, E., 2013. *Surfaces and essences: Analogy as the fuel and fire of thinking*. New York, Basic Books.

Hofstede, G., 1984. The cultural relativity of the quality of life concept. *Academy of Management review*, *9*(3), pp.389-398.

Högl, B., 2017. What the “man in the moon” can tell us about the future of our brains. *Annals of translational medicine*, *5*(17).

Hoicka, E. and Akhtar, N., 2012. Early humour production. *British Journal of Developmental Psychology*, *30*(4), pp.586-603.

Holly Smith, B., Crummett, T.L. and Brandt, K.L., 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *American journal of physical anthropology*, *37*(S19), pp.177-231.

Holtmann, M., Bölte, S. and Poustka, F., 2007. Autism spectrum disorders: Sex differences in autistic behaviour domains and coexisting psychopathology. *Developmental Medicine & Child Neurology*, *49*(5), pp.361-366.

Holyoak, K., Gentner, D. and Kokinov, B., 2001. The place of analogy in cognition.In *The analogical mind: Perspectives from cognitive science*, eds. Gentner, D., Holyoak, K., Kokinov, B.. Cambridge, Ma., MIT Press.

Honeycutt, J.M. and Brown, R., 1998. Did you hear the one about?: Typological and spousal differences in the planning of jokes and sense of humor in marriage. *Communication Quarterly*, *46*(3), pp.342-352.

Hooks, M.S. and Kalivas, P.W., 1995. The role of mesoaccumbens-pallidal circuitry in novelty-induced behavioral activation. *Neuroscience*, *64*(3), pp.587-597.

Hopkins, W.D., Taglialatela, J.P. and Leavens, D.A., 2007. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal behaviour*, *73*(2), pp.281-286.

Hopkins, W.D., Taglialatela, J.P. and Leavens, D.A., 2011. Do chimpanzees have voluntary control of their facial expressions and vocalizations. *Primate communication and human language: Vocalisation, gestures, imitation and deixis in humans and non-humans*, *1*, pp.71-88.

Horner, V. and Whiten, A., 2005. Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal cognition*, *8*(3), pp.164-181.

Hoshikawa, T., 1991. Effects of attention and expectation on tickle sensation. *Perceptual and motor skills*, *72*(1), pp.27-33.

Hovers, E., Ilani, S., Vandermeersch, B., Barham, L., BelferCohen, A., Klein, R., Knight, C., Power, C., Watts, I., McBrearty, S. and Marshack, A., 2003. An early case of color symbolism: ochre use by modern humans in Qafzeh Cave. *Current Anthropology*, *44*(4), pp.491-522.

Howe, N.E., 2002. The origin of humor. *Medical hypotheses*, *59*(3), pp.252-254.

Howrigan, D.P. and MacDonald, K.B., 2008. Humor as a mental fitness indicator. *Evolutionary Psychology*, *6*(4), p.652-666.

Huber, T. and Ruch, W., 2007. Laughter as a uniform category? a historic analysis of different types of laughter. In *10th Congress of the Swiss Society of Psychology. University of Zurich, Switzerland*.

Huitt, W. and Cain, S., 2005. An overview of the conative domain. *Educational psychology interactive*, pp.1-20.

Huizinga, J., 1949. *Homo Ludens: A Study of the Play-element in Cult*ure. London, Routledge & Kegan Paul Ltd.

Huizink, A.C., Robles de Medina, P.G., Mulder, E.J., Visser, G.H. and Buitelaar, J.K., 2003. Stress during pregnancy is associated with developmental outcome in infancy. *Journal of Child Psychology and Psychiatry*, *44*(6), pp.810-818.

Hummel, J.E. and Holyoak, K.J., 2003. A symbolic-connectionist theory of relational inference and generalization. *Psychological review*, *110*(2), p.220.

Humphrey, N., 1999. *A History of the Mind: Evolution and the Birth of Consciousness*. New York, Springer Science & Business Media.

Humphrey, N., 2016. A riddle written on the brain. *Journal of Consciousness Studies*, *23*(7-8), pp.278-287.

Hunt, B.G., Ometto, L., Wurm, Y., Shoemaker, D., Soojin, V.Y., Keller, L. and Goodisman, M.A., 2011. Relaxed selection is a precursor to the evolution of phenotypic plasticity. *Proceedings of the National Academy of Sciences*, *108*(38), pp.15936-15941.

Hurford, J.R., 1999. The evolution of language and languages. In *The evolution of culture*, eds. Dunbar, R., Knight, C., Power, C.. Edinburgh, University of Edinburgh Press, pp.173-93.

Hurford, J.R., 2004. Human uniqueness, learned symbols and recursive thought. *European Review*, *12*(4), pp.551-565.

Hurford, J.R., 2006. Recent developments in the evolution of language. *Cognitive Systems*, *7*(1), pp.23-32.

Hurley, M., 2006. *The joy of debugging: towards a computational model of humor*. Honors dissertation in Cognitive Science, Tufts University, Medford Massachusetts.

Hurley, M.M., Dennett, D.C. and Adams, R.B., 2011. *Inside jokes: Using humor to reverse-engineer the mind*. Cambridge, Ma., MIT Press.

Hurley, S.L. and Chater, N. eds., 2005. *Perspectives on Imitation: Mechanisms of imitation and imitation in animals* (Vol. 1). Cambridge, Ma., MIT Press.

Hutchinson, J.B. and Turk-Browne, N.B., 2012. Memory-guided attention: Control from multiple memory systems. *Trends in cognitive sciences*, *16*(12), pp.576-579.

Iacoboni, M., 2009. Imitation, empathy, and mirror neurons. *Annual review of psychology*, *60*, pp.653-670.

Illnerova, H., Buresova, M. and Presl, J., 1993. Melatonin rhythm in human milk. *The Journal of Clinical Endocrinology & Metabolism*, *77*(3), pp.838-841

Iriki, A., 2006. The neural origins and implications of imitation, mirror neurons and tool use. *Current opinion in neurobiology*, *16*(6), pp.660-667.

Isbell, L.A. and Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. *Journal of human evolution*, *30*(5), pp.389-397.

Iwase, M., Ouchi, Y., Okada, H., Yokoyama, C., Nobezawa, S., Yoshikawa, E., Tsukada, H., Takeda, M., Yamashita, K., Takeda, M. and Yamaguti, K., 2002. Neural substrates of human facial expression of pleasant emotion induced by comic films: a PET study. *Neuroimage*, *17*(2), pp.758-768.

Izard, C.E., 1992. Basic emotions, relations among emotions, and emotion-cognition relations. *Psychological Review*, No. 3., pp. 561-565.

Jablonka, E. and Lamb, M.J., 2007. Précis of evolution in four dimensions. *Behavioral and Brain Sciences*, *30*(4), pp.353-365.

Jack, R.E., Garrod, O.G. and Schyns, P.G., 2014. Dynamic facial expressions of emotion transmit an evolving hierarchy of signals over time. *Current biology*, *24*(2), pp.187-192.

Jackendoff, R., 1995. *Languages of the mind: Essays on mental representation*. Cambridge, Ma., MIT Press.

Jackendoff, R., 2009. Parallels and nonparallels between language and music. *Music Perception: An Interdisciplinary Journal*, *26*(3), pp.195-204.

Jackendoff, R. and Pinker, S., 2005. The nature of the language faculty and its implications for evolution of language (Reply to Fitch, Hauser, and Chomsky). *Cognition*, *97*(2), pp.211-225.

Jaeggi, A.V., Dunkel, L.P., Van Noordwijk, M.A., Wich, S.A., Sura, A.A. and Van Schaik, C.P., 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *American Journal of Primatology*, *72*(1), pp.62-71.

Janik, V.M. and Slater, P.J., 1997. Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, pp.59-100.

Jansen, W.H., 1959. The esoteric-exoteric factor in folklore. *Fabula*, *2*(3), p.205.

Jarvis E.D.*,* Scharff C.*,* Grossman M.R.*,* Ramos J.A.*,* and Nottebohm F. 1998. For whom the bird sings: context-dependent gene expression. *Neuron 21,* pp. 775–788.

Jawahar, M.C., Murgatroyd, C., Harrison, E.L. and Baune, B.T., 2015. Epigenetic alterations following early postnatal stress: a review on novel aetiological mechanisms of common psychiatric disorders. *Clinical epigenetics*, *7*(1), p.122.

Jensen-Campbell, L.A., Graziano, W.G. and West, S.G., 1995. Dominance, prosocial orientation, and female preferences: Do nice guys really finish last?. *Journal of Personality and Social Psychology*, *68*(3), p.427.

Jespersen, O., 1923. *Language: its nature, development and origin*. New York, Holt.

Jespersen, O., 2003. *Essentials of English Grammar*. London, Routledge.

Jitsumori, M. and Delius, J.D., 2008. Object recognition and object categorization in animals. In *Primate origins of human cognition and behavior*. Tokyo, Springer, pp. 269-293.

Johnson, M.H., 2000. Functional brain development in infants: elements of an interactive specialization framework. *Child development*, *71*(1), pp.75-81.

Johnson, M.H., 2001. Functional brain development in humans. *Nature Reviews Neuroscience*, *2*(7), pp.475-483.

Jung, W.E., 2003. The inner eye theory of laughter: Mindreader signals cooperator value. *Evolutionary Psychology*, *1*(1), pp. 214-253.

Kabakian-Khasholian, T., Campbell, O., Shediac-Rizkallah, M. and Ghorayeb, F., 2000. Women's experiences of maternity care: satisfaction or passivity?. *Social science & medicine*, *51*(1), pp.103-113.

Kalant, H., Pinker, S. and Kalow, W., 1997. Evolutionary psychology: An exchange. *Exchange*, *44*(15).

Kampe, K.K., Frith, C.D. and Frith, U., 2003. “Hey John”: signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. *Journal of Neuroscience*, *23*(12), pp.5258-5263.

Kaplan, H.S. & Robson, A.J., 2002. *The emergence of humans: the co-evolution of intelligence and longevity with intergenerational transfers*. Proc. Natl. Acad. Sci. U.S.A. 99, pp. 10221–10226.

Karasev, L.V., 1996. *Filosofiya smecha (Philosophy of Laughter)*. Moscow, RGGU.

Karmiloff-Smith, A., 1992. *Beyond modularity: A developmental approach to cognitive science*. Cambridge, Ma., MIT Press.

Karousou, A. and López-Ornat, S., 2013. Prespeech vocalizations and the emergence of speech: a study of 1005 Spanish children. *The Spanish journal of psychology*, *16*.

Katz, B.F., 1993. A neural resolution of the incongruity-resolution and incongruity theories of humour. *Connection Science*, *5*(1), pp.59-75.

Kaufman, J. C., and Kaufman, A. B., 2004. Applying a creativity framework to animal cognition. *New Ideas in Psychology*, *22*, 143–155.

Kaufman, S.B., Erickson, J., Ramesh, S., Kozbelt, A., Magee, M. and Kaufman, J.C., 2010. What are funny people like. In *annual meeting of the Human Behavior and Evolution Society, Eugene, OR*.

Kaufman, S.B., Kozbelt, A., Bromley, M.L., Miller, G.F., Geher, G. and Miller, G., 2008. The role of creativity and humor in human mate selection. *Mating intelligence: Sex, relationships, and the mind’s reproductive system*, pp.227-262.

Kawakami, K., Takai-Kawakami, K., Tomonaga, M., Suzuki, J., Kusaka, T. and Okai, T., 2006. Origins of smile and laughter: A preliminary study. *Early Human Development*, *82*(1), pp.61-66.

Keane, M.T., 1997. What makes an analogy difficult? The effects of order and causal structure on analogical mapping. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *23*(4), p.946.

Kehily, M.J. and Nayak, A., 1997. 'Lads and laughter': humour and the production of heterosexual hierarchies. *Gender and education*, *9*(1), pp.69-88.

Keith-Spiegel, P., 1972. Early conceptions of humor: Varieties and issues. *The psychology of humor: Theoretical perspectives and empirical issues*, pp.4-39.

Kellogg, W.N. and Kellogg, L.A., 1933. *The ape and the child: a study of environmental influence upon early behavior.* Oxford, Whittlesey House.

Keltner, D., 1995. Signs of appeasement: Evidence for the distinct displays of embarrassment, amusement, and shame. *Journal of personality and social psychology*, *68*(3), p.441.

Kemnitz, T.M., 1973. The cartoon as a historical source. *The Journal of Interdisciplinary History*, *4*(1), pp.81-93.

Keverne, E.B., Martensz, N.D. and Tuite, B., 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, *14*(1-2), pp.155-161.

Khaitovich, P., Enard, W., Lachmann, M. and Pääbo, S., 2006. Evolution of primate gene expression. *Nature Reviews Genetics*, *7*(9), pp.693-702.

Kimata, H., 2004(a). Effect of viewing a humorous vs. nonhumorous film on bronchial responsiveness in patients with bronchial asthma. *Physiology & behavior*, *81*(4), pp.681-684.

Kimata, H., 2004(b). Reduction of plasma levels of neurotrophins by laughter in patients with atopic dermatitis. *Pediatric Asthma, Allergy & Immunology*, *17*(2), pp.131-135.

Kimata, H., 2004(c). Laughter Counteracts Enhancement of Plasma Neurotrophin Levels and Allergic Skin Wheal Responses by Mobile Phone—Mediated Stress. *Behavioral Medicine*, *29*(4), pp.149-154.

Kimata, H., 2004(d). Reduction of allergen-specific IgE production by laughter. *European journal of clinical investigation*, *34*(1), pp.76-77.

Kimata, H., 2007. Laughter elevates the levels of breast-milk melatonin. *Journal of psychosomatic research*, *62*(6), pp.699-702.

Kinde, J., 2009. The rule of three: A humor technique from the world of comedy. Online source: *http://www. humorpower. com/art-rulethree. Html (accessed October 2, 2013).*

Kinsella, A.R., 2010. 10. Was recursion the key step in the evolution of the human language faculty?. *Recursion and human language*, *104*, p.179.

Kirkpatrick, G., 2012. Constitutive tensions of gaming's field: UK gaming magazines and the formation of gaming culture 1981–1995. *Game Studies*, *12*(1).

Kitayama, S., King, A., Yoon, C., Tompson, S., Huff, S. and Liberzon, I., 2014. The dopamine D4 receptor gene (DRD4) moderates cultural difference in independent versus interdependent social orientation. *Psychological Science*, *25*(6), pp.1169-1177.

Kleeman, J.A., 1967. The peek-a-boo game: part I: its origins, meanings, and related phenomena in the first year. In *The psychoanalytic study of the child*, *22*(1), ed. Solnit, A.. New Haven, Conn, Yale University Press, pp.239-273.

Klein, A.J. ed., 2003. *Humor in children's lives: A guidebook for practitioners*. Westport Conn., Praeger.

Klein, R.G. and Edgar, B., 2002. *The dawn of human culture*. New York, Wiley.

Knight, C., 2000. *Play as precursor of phonology and syntax*. In *The evolutionary emergence of language: social function and the origins of linguistic form*, eds., Knight, C., Studdert-Kennedy, M. and Hurford, J.. Cambridge, Cambridge University Press, pp. 99-120.

Knight, C., Studdert-Kennedy, M. and Hurford, J.R., 2000. *Language: a Darwinian adaptation*. Cambridge, Cambridge University Press, pp. 1-15.

Knight, C., Studdert-Kennedy, M. and Hurford, J. eds., 2000. *The evolutionary emergence of language: social function and the origins of linguistic form*. Cambridge, Cambridge University Press.

Ko, H.J. and Youn, C.H., 2011. Effects of laughter therapy on depression, cognition and sleep among the community-dwelling elderly. *Geriatrics & Gerontology International*, *11*(3), pp.267-274.

Koestler, A., 1964. *The act of creation: A study of conscious and unconscious processes of humor, scientific discovery and art*. Macmillan Company.

Köhler, W., 2013. *The mentality of apes*. London, Routledge.

Kohn, N., Kellermann, T., Gur, R.C., Schneider, F. and Habel, U., 2011. Gender differences in the neural correlates of humor processing: implications for different processing modes. *Neuropsychologia*, *49*(5), pp.888-897.

Kojima, S. and Kiritani, S., 1989. Vocal-auditory functions in the chimpanzee: vowel perception. *International Journal of Primatology*, *10*(3), pp.199-213.

Kojima, S., Tatsumi, I.F., Kiritani, S. and Hirose, H., 1989. Vocal-auditory functions of the chimpanzee: consonant perception. *Human Evolution*, *4*(5), pp.403-416.

Korczynski, M., 2011. The dialectical sense of humour: Routine joking in a Taylorized factory. *Organization Studies*, *32*(10), pp.1421-1439.

Kozintsev, A., 2011. *The mirror of laughter* (Vol. 1). New York, Transaction Publishers.

Krishnan, H.S. and Chakravarti, D., 2003. A process analysis of the effects of humorous advertising executions on brand claims memory. *Journal of consumer psychology*, *13*(3), pp.230-245.

Kroeber, A.L. and Kluckhohn, C., 1952. Culture: A critical review of concepts and definitions. *Papers. Peabody Museum of Archaeology & Ethnology, Harvard University*.

Krolak-Salmon, P., Hénaff, M.A., Vighetto, A., Bauchet, F., Bertrand, O., Mauguiere, F. and Isnard, J., 2006. Experiencing and detecting happiness in humans: the role of the supplementary motor area. *Annals of neurology*, *59*(1), pp.196-199.

Krutnik, F. and Neale, S., 2006. *Popular film and television comedy*. London, Routledge.

Kubie, L.S., 1971. The destructive potential of humor in psychotherapy. *American Journal of Psychiatry*, *127*(7), pp.861-866.

Kuhn, C.C., 1994. The stages of laughter. *Journal of Nursing Jocularity*, *4*(2), pp.34-35.

Kuiper, N.A., 2012. Humor and resiliency: Towards a process model of coping and growth. *Europe's Journal of Psychology*, *8*(3), pp.475-491.

Kuiper, N.A., Martin, R.A. and Dance, K.A., 1992. Sense of humour and enhanced quality of life. *Personality and individual differences*, *13*(12), pp.1273-1283.

Lahti, D.C., Johnson, N.A., Ajie, B.C., Otto, S.P., Hendry, A.P., Blumstein, D.T., Coss, R.G., Donohue, K. and Foster, S.A., 2009. Relaxed selection in the wild. *Trends in ecology & evolution*, *24*(9), pp.487-496.

Lai, C.S., Fisher, S.E., Hurst, J.A., Vargha-Khadem, F. and Monaco, A.P., 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature*, *413*(6855), p.519.

Lakoff, G., 1993. The contemporary theory of metaphor. In *Metaphor and thought,* ed. by Andrew Ortony, Cambridge, Cambridge University Press, pp.202-251.

Lakoff, G. and Johnson, M., 2008. *Metaphors we live by*. Chicago, University of Chicago Press.

Laland, K.N. and Janik, V.M., 2006. The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), pp.542-547.

Langer, S.K., 1953. *Feeling and form*, London, Routledge and Kegan Paul.

Laplante, D.P., Barr, R.G., Brunet, A., Du Fort, G.G., Meaney, M.L., Saucier, J.F., Zelazo, P.R. and King, S., 2004. Stress during pregnancy affects general intellectual and language functioning in human toddlers. *Pediatric research*, *56*(3), pp.400-410.

Lass, R., 1990. How to do things with junk: exaptation in language evolution1. *Journal of linguistics*, *26*(1), pp.79-102.

Lau, E.F., Phillips, C. and Poeppel, D., 2008. A cortical network for semantics:(de) constructing the N400. *Nature Reviews Neuroscience*, *9*(12), pp.920-933.

Laucht, M., Becker, K., Blomeyer, D. and Schmidt, M.H., 2007. Novelty seeking involved in mediating the association between the dopamine D4 receptor gene exon III polymorphism and heavy drinking in male adolescents: results from a high-risk community sample. *Biological psychiatry*, *61*(1), pp.87-92.

Launay, J., Tarr, B. and Dunbar, R.I., 2016. Synchrony as an Adaptive Mechanism for Large-Scale Human Social Bonding. *Ethology*, *122*(10), pp.779-789.

Lavery, D., 2005. Aesop After Darwin: The Radical Anthropomorphism of" The Far Side". *Studies in Popular Culture*, *28*(1), pp.71-83.

Lazarus, R.S., Kanner, A.D. and Folkman, S., 1980. Emotions: A cognitive-phenomenological analysis. *Theories of emotion*, *1*, pp.189-217.

Leakey, R., 2008. *The origin of humankind*. New York, Basic Books.

Leavens, D.A., 2009. Animal communication: laughter is the shortest distance between two apes. *Current Biology*, *19*(13), pp.R511-R513.

Leavens, D.A. and Racine, T.P., 2009. Joint attention in apes and humans: are humans unique? *Journal of Consciousness Studies*, *16*(6-1), pp.240-267.

LeBlanc, A., Sims, W.L., Malin, S.A. and Sherrill, C., 1992. Relationship between humor perceived in music and preferences of different-age listeners. *Journal of Research in Music Education*, *40*(4), pp.269-282.

Lebowitz, K.R., Suh, S., Diaz, P.T. and Emery, C.F., 2011. Effects of humor and laughter on psychological functioning, quality of life, health status, and pulmonary functioning among patients with chronic obstructive pulmonary disease: a preliminary investigation. *Heart & Lung: The Journal of Acute and Critical Care*, *40*(4), pp.310-319.

Leekam, S.R., 1991. Jokes and lies: Children's understanding of intentional falsehood. *Natural theories of mind: Evolution, development and simulation of everyday mindreading, ed,. White, A.*. Cambridge, MA, US: Basil Blackwell, pp. 159-174.

Lefcourt, H.M., 2001. *Humor: The psychology of living buoyantly*. New York, Springer Science & Business Media.

Lefcourt, H.M., Davidson-Katz, K. and Kueneman, K., 1990. Humor and immune-system functioning. *Humor - International Journal of Humor Research*, 3(3), pp. 305-322.

Lefcourt, H.M. and Martin, R.A., 2012. *Humor and life stress: Antidote to adversity*. New York, Springer Science & Business Media.

Lefebvre, L., 2000. Feeding innovations and their cultural transmission in bird populations. *The evolution of cognition*, pp.311-328.

Lei, S.A., Cohen, J.L. and Russler, K.M., 2010. Humor on learning in the college classroom: Evaluating benefits and drawbacks from instructors' perspectives. *Journal of Instructional Psychology*, *37*(4), pp.326-332.

Leigh, S.R., 2004. Brain growth, life history, and cognition in primate and human evolution. *American journal of primatology*, *62*(3), pp.139-164.

Leonhard, D. and Brugger, P., 1998. Creative, Paranormal, and Delusional Thought: A Consequence of Right Hemisphere Semantic Activation?. *Cognitive and Behavioral Neurology*, *11*(4), pp.177-183.

Leslie, A.M., 1987. Pretense and representation: The origins of" theory of mind.". *Psychological review*, *94*(4), p.412.

Leslie, A.M., 1994. ToMM, ToBy, and Agency: Core architecture and domain-specificity. *Mapping the mind: Domain-specificity in cognition and culture*, pp.119-148.

Leslie, K.R., Johnson-Frey, S.H. and Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. *Neuroimage*, *21*(2), pp.601-607.

Leuba, C., 1941. Tickling and laughter: Two genetic studies. *The Pedagogical Seminary and Journal of Genetic Psychology*, *58*(1), pp.201-209.

Levi, L., 1965. The urinary output of adrenalin and noradrenalin during pleasant and unpleasant emotional states: A preliminary report. *Psychosomatic Medicine*, *27*(1), pp.80-85.

Levin, M. and Ward, T.N., 2003. Laughing headache: a novel type of triggered headache with response to divalproex sodium. *Headache: The Journal of Head and Face Pain*, *43*(7), pp.801-803.

Levins, R., 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *The American Naturalist*, *96*(891), pp.361-373.

Lewis, M., 2012. *Social cognition and the acquisition of self*. New York, Springer Science & Business Media.

Lewis, M., Stanger, C. and Sullivan, M.W., 1989. Deception in 3-year-olds. *Developmental psychology*, *25*(3), p.439.

Li, N.P., Balley, J.M., Kenrick, D.T. and Linsenmeier, J.A., 2002. The necessities and luxuries of mate preferences: Testing the tradeoffs. *Journal of personality and social psychology*, *82*(6), pp.947-955.

Li, N.P., Griskevicius, V., Durante, K.M., Jonason, P.K., Pasisz, D.J. and Aumer, K., 2009. An evolutionary perspective on humor: sexual selection or interest indication?. *Personality and Social Psychology Bulletin*, *35*(7), pp.923-936.

Lieberman, P., Laitman, J.T., Reidenberg, J.S. and Gannon, P.J., 1992. The anatomy, physiology, acoustics and perception of speech: essential elements in analysis of the evolution of human speech. *Journal of Human Evolution*, *23*(6), pp.447-467.

Liu, J., Li, J., Feng, L., Li, L., Tian, J. and Lee, K., 2014. Seeing Jesus in toast: neural and behavioral correlates of face pareidolia. *Cortex*, *53*, pp.60-77.

Livak, K.J., Rogers, J. and Lichter, J.B., 1995. Variability of dopamine D4 receptor (DRD4) gene sequence within and among nonhuman primate species. *Proceedings of the National Academy of Sciences*, *92*(2), pp.427-431.

Locke, E.A., 1927. Five cases of spontaneous rupture of the heart. *The Boston Medical and Surgical Journal*, *197*(21), pp.955-961.

Logan, R.K., 1995. *The fifth language: Learning a living in the computer age*. Toronto, Stoddart.

Logan, R.K., 2000. *Sixth Language: Learning a Living in the Internet Age*. Toronto, Stoddart.

Logan, R.K., 2006. The extended mind model of the origin of language and culture. In *Evolutionary epistemology, language and culture*. Amsterdam, Springer, pp. 149-167.

Lorenz, K., 1963. *On aggression*. NewYork, Harcourt.

Lorenz, K., 2002. *Man meets dog*. New Delhi, Routledge.

Lovejoy, M.C., Graczyk, P.A., O'Hare, E. and Neuman, G., 2000. Maternal depression and parenting behavior: A meta-analytic review. *Clinical psychology review*, *20*(5), pp.561-592.

Lundy, D.E., Tan, J. and Cunningham, M.R., 1998. Heterosexual romantic preferences: The importance of humor and physical attractiveness for different types of relationships. *Personal Relationships*, *5*(3), pp.311-325.

Lynch, O.H., 2002. Humorous communication: Finding a place for humor in communication research. *Communication theory*, *12*(4), pp.423-445.

Lyons, V. and Fitzgerald, M., 2004. Humor in autism and Asperger syndrome. *Journal of autism and developmental disorders*, *34*(5), pp.521-531.

MacNeilage, P.F. and Davis, B.L., 2000. Deriving speech from nonspeech: A view from ontogeny. *Phonetica*, *57*(2-4), pp.284-296.

Maddieson, I. and Precoda, K., 1989. Updating upsid. *The Journal of the Acoustical Society of America*, *86*(S1), pp.S19-S19.

Maier, N.R., 1932. A Gestalt theory of humour. *British Journal of Psychology. General Section*, *23*(1), pp.69-74.

Malefijt, A.W., 1968. Dutch joking patterns. *Transactions of the New York Academy of Sciences*, *30*(8 Series II), pp.1181-1186.

Malinowski, Bronislaw. 1937. "Introduction." In *The savage hits back, or the white man through native eyes*, by Julius E. Lips, vii–ix. London, Lovat Dickinson.

Malone, N., Fuentes, A. and White, F.J., 2012. Variation in the social systems of extant hominoids: comparative insight into the social behavior of early hominins. *International Journal of Primatology*, *33*(6), pp.1251-1277.

Malotki, E. and Wallace, H.D., 2011. Columbian mammoth petroglyphs from the San Juan River near Bluff, Utah, United States. *Rock Art Research: The Journal of the Australian Rock Art Research Association (AURA)*, *28*(2), p.143.

Manninen, S., Tuominen, L., Dunbar, R., Karjalainen, T., Hirvonen, J., Arponen, E., Hari, R., Jääskeläinen, I.P., Sams, M. and Nummenmaa, L., 2017. Social laughter triggers endogenous opioid release in humans. *Journal of Neuroscience*, pp.0688-16.

Mantonakis, A., Bernstein, D.M. and Loftus, E.F., 2011. Attributions of fluency: Familiarity, preference, and the senses. In *Constructions of Remembering and Metacognition* (pp. 40-50). London, Palgrave Macmillan.

Marcus, S.M., 2009. Depression during pregnancy: rates, risks and consequences. *Can J Clin Pharmacol*, *16*(1), pp.15-22.

Margolis, E. and Laurence, S., "Concepts", *The Stanford Encyclopedia of Philosophy,* Spring 2014 Edition, Edward N. Zalta (ed.), Online edition: https://plato.stanford.edu/archives/spr2014/entries/concepts/

Markus, N. and Croft, D.B., 1995. Play behaviour and its effects on social development of common chimpanzees (Pan troglodytes). *Primates*, *36*(2), pp.213-225.

Marler, P. and Hobbett, L., 1975. Individuality in a Long-Range Vocalization of Wild Chimpanzees. *Ethology*, *38*(1), pp.97-109.

Marshack, A., 1976. Some implications of the Paleolithic symbolic evidence for the origin of language. *Current Anthropology*, *17*(2), pp.274-282.

Martin, R.A., 1998. Approaches to the sense of humor: A historical review. *The sense of humor: Explorations of a personality characteristic*, pp.15-60.

Martin, R.A., 2010. *The psychology of humor: An integrative approach*. New York, Academic Press.

Martin, R.A. and Kuiper, N.A., 1999. Daily occurrence of laughter: Relationships with age, gender, and Type A personality. *Humor*, *12*(4), pp.355-384.

Martin, R.A., Puhlik-Doris, P., Larsen, G., Gray, J. and Weir, K., 2003. Individual differences in uses of humor and their relation to psychological well-being: Development of the Humor Styles Questionnaire. *Journal of research in personality*, *37*(1), pp.48-75.

Martin-Ordas, G., Haun, D., Colmenares, F. and Call, J., 2010. Keeping track of time: evidence for episodic-like memory in great apes. *Animal cognition*, *13*(2), pp.331-340.

Martineau, W.H., 1972. A model of the social functions of humor.In *The psychology of humor: Theoretical perspectives and empirical issues*, ed., Goldstein, J.. New York, Academic Press, pp.101-125.

Maslow, A.H., 1943. A theory of human motivation. *Psychological review*, *50*(4), p.370.

Masten, A.S., 1986. Humor and competence in school-aged children. *Child development*, pp.461-473.

Matsumoto, D., Keltner, D., Shiota, M.N., O'Sullivan, M. and Frank, M., 2008. Facial expressions of emotion. In *Handbook of emotions*, *3*, eds., Lewis, M., Haviland-Jones, J., Feldman-Barrett, L.. London, Guilford Press, pp.211-234.

Matsunobu, K., 2011. Pedagogy of imitation and repetition. In *The Routledge international handbook of creative learning*, eds., Sefton-Green, J., Thomson, P., Jones, K. and Bresler, L. London, Routledge,pp.45-53.

Matsuzaki, T., Nakajima, A., Ishigami, S., Tanno, M. and Yoshino, S., 2005. Mirthful laughter differentially affects serum pro-and anti-inflammatory cytokine levels depending on the level of disease activity in patients with rheumatoid arthritis. *Rheumatology*, *45*(2), pp.182-186.

Matsuzawa, T., 2008. Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In *Primate origins of human cognition and behavior* (pp. 3-25). Tokyo, Springer.

Matthews LJ, Butler PM. 2011. Novelty-seeking DRD4 polymorphisms are associated with human migration distance out-of-Africa after controlling for neutral population gene structure. *Am J Phys Anthropol 145*: pp.382–389.

Maurer, A., 1969. Peek-a-boo: An entry into the world of the autistic child. *The Journal of Special Education*, *3*(3), pp.309-312.

Maus, F.E., 1991. Music as narrative. *Indiana theory review*, *12*, pp.1-34.

Mayer, D.E.B.Y., Vandermeersch, B. and Bar-Yosef, O., 2009. Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: indications for modern behavior. *Journal of Human Evolution*, *56*(3), pp.307-314.

McBrearty, S. and Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of human evolution*, *39*(5), pp.453-563.

McCauley, B., Maxwell, D. and Collard, M., 2018. A Cross-cultural Perspective on Upper Palaeolithic Hand Images with Missing Phalanges. *Journal of Paleolithic Archaeology*, pp.1-20.

McComas, H.C., 1923. The Origin of Laughter. *Psychological Review*, *30*(1), p.45.

McCrae, R.R. and Costa, P.T., 1987. Validation of the five-factor model of personality across instruments and observers. *Journal of personality and social psychology*, *52*(1), p.81.

McDermott, J. and Hauser, M.D., 2005. The origins of music: Innateness, uniqueness, and evolution. *Music Perception: An Interdisciplinary Journal*, *23*(1), pp.29-59.

McDermott, J. and Hauser, M.D., 2007. Nonhuman primates prefer slow tempos but dislike music overall. *Cognition*, *104*(3), pp.654-668.

McDermott, L., 1996. Self-representation in Upper Paleolithic female figurines. *Current Anthropology*, *37*(2), pp.227-275.

McDougall, W., 1903. The theory of laughter. *Nature*, *67*(3), p.1.

McGhee, P.E., 1971. Cognitive development and children's comprehension of humor. *Child Development*, pp.123-138.

McGhee, P.E., 1976. Children's appreciation of humor: A test of the cognitive congruency principle. *Child Development*, pp.420-426.

McGhee, P.E., 1979. *Humor, its origin and development*. New York, W.H. Freeman.

McGhee, P.E., 1980. Development of the sense of humour in childhood: A longitudinal study. *Children's humour*, pp.213-236.

McGhee, P.E., 2015. The playful brain: Development of young children's humour. *Educating Young Children: Learning and Teaching in the Early Childhood Years*, *21*(2), p.20.

McGee, P.E. and Shevlin, M., 2009. Effect of humor on interpersonal attraction and mate selection. *The Journal of psychology*, *143*(1), pp.67-77.

McKellar, P., 1957. *Imagination and thinking: A psychological analysis*. Oxford, England, Basic Books.

McKenzie, S., Frank, A.J., Kinsky, N.R., Porter, B., Rivière, P.D. and Eichenbaum, H., 2014. Hippocampal representation of related and opposing memories develop within distinct, hierarchically organized neural schemas. *Neuron*, *83*(1), pp.202-215.

Mehu, M., 2011. Smiling and laughter in naturally occurring dyadic interactions: Relationship to conversation, body contacts, and displacement activities. *Human Ethology Bulletin*, *26*(1), pp.10-28.

Mehu, M. and Dunbar, R.I., 2008. Relationship between smiling and laughter in humans (Homo sapiens): Testing the power asymmetry hypothesis. *Folia Primatologica*, *79*(5), pp.269-280.

Meltzoff, A.N., 1985. The roots of social and cognitive development: Models of man's original nature. *Social perception in infants*, pp.1-30.

Meltzoff, A.N., 1988. Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental psychology*, *24*(4), p.470.

Meltzoff, A.N., 1988. Infant imitation and memory: Nine-month-olds in immediate and deferred tests. *Child development*, *59*(1), p.217.

Meltzoff, A.N., 1990. Foundations for developing a concept of self: The role of imitation in relating self to other and the value of social mirroring, social modeling, and self practice in infancy. In *The John D. and Catherine T. MacArthur foundation series on mental health and development. The self in transition: Infancy to childhood, eds.* Cicchetti, D., and Beeghly, M.. Chicago, University of Chicago Press, pp. 139-164.

Meltzoff, A.N., 1993. The role of imitation in understanding persons and developing a theory of mind. In *Understanding other minds: Perspectives from autism*, eds., Baron-Cohen, S.E., Tager-Flusberg, H.E. and Cohen, D.J., 1994. Oxford, Oxford University Press.

Meltzoff, A.N., 2002. Imitation as a mechanism of social cognition: Origins of empathy, theory of mind, and the representation of action. *Blackwell handbook of childhood cognitive development*, pp.6-25.

Meltzoff, A.N. and Decety, J., 2003. What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*(1431), pp.491-500.

Meltzoff, A.N. and Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. *Science*, *198*(4312), pp.75-78.

Meltzoff, A.N. and Moore, M.K., 2002. Imitation, memory, and the representation of persons. *Infant behavior and development*, *25*(1), pp.39-61.

Mendoza-Granados, D. and Sommer, V., 1995. Play in chimpanzees of the Arnhem Zoo: Self-serving compromises. *Primates*, *36*(1), pp.57-68.

Menon, V. and Levitin, D.J., 2005. The rewards of music listening: response and physiological connectivity of the mesolimbic system. *Neuroimage*, *28*(1), pp.175-184.

Menzel, C.R., 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. *Journal of Comparative Psychology*, *113*(4), p.426.

Merker, B., 2000. Synchronous chorusing and the origins of music. *Musicae Scientiae*, *3*(1 suppl), pp.59-73.

Merrick, N.J., 1977. Social grooming and play behavior of a captive group of chimpanzees. *Primates*, *18*(1), pp.215-224.

Meyer, J.C., 2000. Humor as a double-edged sword: Four functions of humor in communication. *Communication theory*, *10*(3), pp.310-331.

Miles, H.L., 1983. Apes and language: The search for communicative competence. In *Language in primates* . New York, Springer, pp. 43-61.

Miles, H.L., 1986. How can I tell a lie? Apes, language, and the problem of deception. In *Deception: Perspectives on human and nonhuman deceit*, eds., Mitchell, R.W. and Thompson, N.S.. New York, SUNY Press, pp.245-266.

Miles, H.L., 1991. The development of symbolic communication in apes and early hominids. *Studies in language origins*, *2*.

Miles, H.L., 1999. Symbolic communication with and by great apes. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentalities of gorillas and orangutans: Comparative perspectives* New York, NY, US: Cambridge University Press, pp. 197-210.

Miller, G., 1998. A review of sexual selection and human evolution: How mate choice shaped human nature. *Handbook of evolutionary psychology: ideas, issues, and applications.* New Jersey, Lawrence Erlbaum, pp.87-130.

Miller, G., 2000(a). Evolution of human music through sexual selection. In *The Origins of Music*, eds. Wallin, N.L., Merker, B. and Brown, S. Cambridge, Ma, MIT press, pp. 329-360.

Miller, G., 2000(b). Sexual selection for indicators of intelligence. In *Novartis Foundation Symposium* (pp. 260-270). Chichester; New York; John Wiley.

Miller, G., 2011. *The mating mind: How sexual choice shaped the evolution of human nature*. New York, Anchor.

Miller, K.D., 1996. Synaptic economics: competition and cooperation in synaptic plasticity. *Neuron*, *17*(3), pp.371-374.

Miller, M. and Fry, W.F., 2009. The effect of mirthful laughter on the human cardiovascular system. *Medical hypotheses*, *73*(5), pp.636-639.

Miller, N.E. and Dollard, J., 2013. *Social learning and imitation. Ils 254* (Vol. 14). London, Routledge.

Milner, G.B., 1972. Homo ridens. Towards a semiotic theory of humour and laughter. *Semiotica*, *5*(1), pp.1-30.

Mintz, L.E., 1985. Standup comedy as social and cultural mediation. *American Quarterly*, *37*(1), pp.71-80.

Mintz, T., 1967. Tickle--the Itch That Moves: A Psychophysiological Hypothesis. *Psychosomatic medicine*, *29*(6), pp.606-611.

Mireault, G., Sparrow, J., Poutre, M., Perdue, B. and Macke, L., 2012. Infant humor perception from 3-to 6-months and attachment at one year. *Infant Behavior and Development*, *35*(4), pp.797-802.

Mireault, G., Poutre, M., Sargent-Hier, M., Dias, C., Perdue, B. and Myrick, A., 2012. Humour perception and creation between parents and 3-to 6-month-old infants. *Infant and Child Development*, *21*(4), pp.338-347.

Mithen, S., 1996. *The prehistory of the mind: a search for the origins of art, science and religion.* London and New York, Thames and Hudson.

Mithen, S., 2005. *The singing Neanderthals: The origin of language, music, mind and body*. London, Weidenfeld and Nicolson.

Mithen, S., 2008. Singing in the brain. *New Scientist*, *197*(2644), pp.38-39.

Mizuno, Y., & Takeshita, H., 2002. Behavioral development of chimpanzees in the first month of life: Observation of mother-infant pairs at night. *Japanese Psychological Review*, 45, 352–364.

Mobbs, D., Greicius, M.D., Abdel-Azim, E., Menon, V. and Reiss, A.L., 2003. Humor modulates the mesolimbic reward centers. *Neuron*, *40*(5), pp.1041-1048.

Molineux, C., 2014, July. Understanding the Foundations and Devices in Humour to Determine Practical Design Methods for Systems That Create and/or Detect Humour in Video Games, Robots and other Forms of Artificial Intelligence. In *International Conference on Intelligent Technologies for Interactive Entertainment* (pp. 99-108). Springer.

Molineux, C., 2016. Life memory archive translation performance memory archive life: textual self-documentation in stand-up comedy. *Comedy Studies*, *7*(1), pp.2-12.

Mondloch, C.J., Lewis, T.L., Budreau, D.R., Maurer, D., Dannemiller, J.L., Stephens, B.R. and Kleiner-Gathercoal, K.A., 1999. Face perception during early infancy. *Psychological Science*, *10*(5), pp.419-422.

Monro, D. H., 1988. "Theories of Humor." From *Writing and Reading Across the Curriculum* 3rd ed. Eds., Behrens, L., and Rosen, L.. Glenview, IL, Scott, Foresman and Company, pp. 349-55.

Moore, B.R., 1992. Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour*, *122*(3), pp.231-263.

Morgan, A.J. and Jorm, A.F., 2008. Self-help interventions for depressive disorders and depressive symptoms: a systematic review. *Annals of general psychiatry*, *7*(1), p.13.

Morgan, T.J.H., Uomini, N.T., Rendell, L.E., Chouinard-Thuly, L., Street, S.E., Lewis, H.M., Cross, C.P., Evans, C., Kearney, R., De La Torre, I. and Whiten, A., 2015. Experimental evidence for the co-evolution of hominin tool making teaching and language. *Nature communications*, *6*.

Morreall, J. (ed.), 1989. The Philosophy of Laughter and Humor. New York, State University of New York Press.

Morreall, J., 1989. Enjoying incongruity. *Humor-International Journal of Humor Research*, *2*(1), pp.1-18.

Morreall, J., 2011. *Comic relief: A comprehensive philosophy of humor* (Vol. 27). New York, John Wiley & Sons.

Morris, R.G.M., 2006. Elements of a neurobiological theory of hippocampal function: the role of synaptic plasticity, synaptic tagging and schemas. *European Journal of Neuroscience*, *23*(11), pp.2829-2846.

Morton, J. and Johnson, M.H., 1991. CONSPEC and CONLERN: a two-process theory of infant face recognition. *Psychological review*, *98*(2), p.164.

Mulder, E.J., De Medina, P.R., Huizink, A.C., Van den Bergh, B.R., Buitelaar, J.K. and Visser, G.H., 2002. Prenatal maternal stress: effects on pregnancy and the (unborn) child. *Early human development*, *70*(1), pp.3-14.

Mulder, M.P. and Nijholt, A., 2002. *Humour research: State of art* (No. TR-CTIT-02-34). University of Twente, Centre for Telematics and Information Technology.

Mullen, B., Brown, R. and Smith, C., 1992. Ingroup bias as a function of salience, relevance, and status: An integration. *European Journal of Social Psychology*, *22*(2), pp.103-122.

Munakata, Y. and Pfaffly, J., 2004. Hebbian learning and development. *Developmental Science*, *7*(2), pp.141-148.

Mundy, P., Sigman, M. and Kasari, C., 1990. A longitudinal study of joint attention and language development in autistic children. *Journal of Autism and developmental Disorders*, *20*(1), pp.115-128.

Murdock, G.P., 1965. *Social structure*, No. 301.4 M8. New York, Free Press.

Murdock, M.C. and Ganim, R.M., 1993. Creativity and humor: Integration and incongruity. *The Journal of Creative Behavior*, *27*(1), pp.57-70.

Murstein, B.I. and Brust, R.G., 1985. Humor and interpersonal attraction. *Journal of personality assessment*, *49*(6), pp.637-640.

Nagell, K., Olguin, R.S. and Tomasello, M., 1993. Processes of social learning in the tool use of chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Journal of Comparative Psychology*, *107*(2), p.174.

Nakamura, T., Matsui, T., Utsumi, A., Yamazaki, M., Makita, K., Harada, T., Tanabe, H.C. and Sadato, N., 2017. The role of the amygdala in incongruity resolution: the case of humor comprehension. *Social neuroscience*, pp.1-13.

Navarrete, A., van Schaik, C.P. and Isler, K., 2011. Energetics and the evolution of human brain size. *Nature*, *480*(7375), p.91.

Nazareth, B.J., 2008. *The Psychology of Military Humour*. New Delhi, Lancer Publishers LLC.

Neisser, U., Boodoo, G., Bouchard Jr, T.J., Boykin, A.W., Brody, N., Ceci, S.J., Halpern, D.F., Loehlin, J.C., Perloff, R., Sternberg, R.J. and Urbina, S., 1996. Intelligence: Knowns and unknowns. *American psychologist*, *51*(2), p.77.

Neitz, M.J., 1980. Humor, hierarchy, and the changing status of women. *Psychiatry*, *43*(3), pp.211-223.

Nelson, E.E. and Panksepp, J., 1998. Brain substrates of infant–mother attachment: contributions o - pioids, oxytocin, and norepinephrine. *Neuroscience & Biobehavioral Reviews*, *22*(3), pp.437-452.

Nelson, S.M., 1990. Diversity of the Upper Paleolithic "Venus Figurines and Archeological Mythology". *Archeological Papers of the American Anthropological Association*, *2*(1), pp.11-22.

Newman, B., O'Grady, M.A., Ryan, C.S. and Hemmes, N.S., 1993. Pavlovian conditioning of the tickle response of human subjects: Temporal and delay conditioning. *Perceptual and Motor Skills*, *77*(3), pp.779-785.

Newmeyer, F.J., 1991. Functional explanation in linguistics and the origins of language. *Language & Communication*, *11*(1-2), pp.3-28.

Nezu, A.M., Nezu, C.M. and Blissett, S.E., 1988. Sense of humor as a moderator of the relation between stressful events and psychological distress: A prospective analysis. *Journal of Personality and social Psychology*, *54*(3), p.520.

Norrick, N.R., 2004. Non-verbal humor and joke performance. *Humor-International Journal of Humor Research*, *17*(4), pp.401-409.

North, M., 2009. *Machine-age comedy* (Vol. 2). Oxford, Oxford University Press.

Nowell, A., 2015. Children, Metaphorical Thinking and Upper Paleolithic Visual Cultures. *Childhood in the Past*, *8*(2), pp.122-132.

Nowell, A., 2017. Visual Cultures in the Upper Palaeolithic. *Cambridge Archaeological Journal*, pp.1-8.

Nummenmaa, L. and Tuominen, L., 2017. Opioid system and human emotions. *British Journal of Pharmacology*.

Nummenmaa, L., Manninen, S., Tuominen, L., Hirvonen, J., Kalliokoski, K.K., Nuutila, P., Jääskeläinen, I.P., Hari, R., Dunbar, R.I. and Sams, M., 2015. Adult attachment style is associated with cerebral μ-opioid receptor availability in humans. *Human brain mapping*, *36*(9), pp.3621-3628.

Nummenmaa, L., Tuominen, L., Dunbar, R., Hirvonen, J., Manninen, S., Arponen, E., Machin, A., Hari, R., Jääskeläinen, I.P. and Sams, M., 2016. Social touch modulates endogenous μ-opioid system activity in humans. *NeuroImage*, *138*, pp.242-247.

Nwokah, E.E., Hsu, H.C., Davies, P. and Fogel, A., 1999. The integration of laughter and speech in vocal communication: A dynamic systems perspective. *Journal of Speech, Language, and Hearing Research*, *42*(4), pp.880-894.

Nyberg, L., 2005. Any novelty in hippocampal formation and memory?. *Current opinion in neurology*, *18*(4), pp.424-428.

O'Donnell-Trujillo, N. and Adams, K., 1983. Heheh in conversation: Some coordinating accomplishments of laughter. *Western Journal of Communication (includes Communication Reports)*, *47*(2), pp.175-191.

Ohala, J.J., Hinton, L. and Nichols, J., 1997, August. Sound symbolism. In *Proc. 4th Seoul International Conference on Linguistics [SICOL]* (pp. 98-103).

Olaniyan, T. and Quayson, A. eds., 2007. *African literature: an anthology of criticism and theory*. New York, Blackwell Pub..

Olins Alpert, B. and Vigier, A., 1992. Des preuves de sens ludique dans l'art au pléistocène supérieur. *L'Anthropologie*, *96*(2-3), pp.219-244.

Olshausen, B.A., Anderson, C.H. and Van Essen, D.C., 1993. A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *Journal of Neuroscience*, *13*(11), pp.4700-4719.

Oring, E., 2010. *Engaging humor*. Chicago, University of Illinois Press.

Ostgaard, H.C., Andersson, G.B.J. and Karlsson, K., 1991. Prevalence of back pain in pregnancy. *Spine*, *16*(5), pp.549-552.

Otmakhova, N., Duzel, E., Deutch, A.Y. and Lisman, J., 2013. The hippocampal-VTA loop: the role of novelty and motivation in controlling the entry of information into long-term memory. In *Intrinsically Motivated Learning in Natural and Artificial Systems*. Berlin Heidelberg, Springer, pp. 235-254.

Otto, J.H., 1994. Effects of probabilistic judgments on negative moods. *Zeitschrift fur experimentelle und angewandte Psychologie*, *41*(2), pp.232-260.

Owren, M.J., and Bacherowski, J.A., 2001. The evolution of emotional expression: a 'selfish-gene' account of smiling and laughter in early hominids and humans. In *Emotion: Current Issues and Future Directions* Mayne TJ, Bonanno GA, eds., New York, Guilford, pp 152–191.

Owren, M.J. and Bachorowski, J.A., 2003. Reconsidering the evolution of nonlinguistic communication: The case of laughter. *Journal of Nonverbal Behavior*, *27*(3), pp.183-200.

Paldam, M., 2000. Social capital: one or many? Definition and measurement. *Journal of economic surveys*, *14*(5), pp.629-653.

Palombit, R.A., Cheney, D.L. and Seyfarth, R.M., 1999. Male grunts as mediators of social interaction with females in wild chacma baboons (Papio cynocephalus ursinus). *Behaviour*, *136*(2), pp.221-242.

Pang, J.F., Kluetsch, C., Zou, X.J., Zhang, A.B., Luo, L.Y., Angleby, H., Ardalan, A., Ekström, C., Sköllermo, A., Lundeberg, J. and Matsumura, S., 2009. mtDNA data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular biology and evolution*, *26*(12), pp.2849-2864.

Panger, M.A., Brooks, A.S., Richmond, B.G. and Wood, B., 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology: Issues, News, and Reviews*, *11*(6), pp.235-245.

Panksepp, J., 1998. The periconscious substrates of consciousness: Affective states and the evolutionary origins of the SELF. *Journal of consciousness studies*, *5*(5-6), pp.566-582.

Panksepp, J. and Burgdorf, J., 2003. "Laughing" rats and the evolutionary antecedents of human joy? *Physiology & behavior*, *79*(3), pp.533-547.

Panksepp, J., Herman, B.H., Vilberg, T., Bishop, P. and DeEskinazi, F.G., 1981. Endogenous opioids and social behavior. *Neuroscience & Biobehavioral Reviews*, *4*(4), pp.473-487.

Paquette, D., Carbonneau, R., Dubeau, D., Bigras, M. and Tremblay, R.E., 2003. Prevalence of father-child rough-and-tumble play and physical aggression in preschool children. *European Journal of Psychology of Education*, *18*(2), pp.171-189.

Parker, S.T., 1996. Apprenticeship in tool-mediated extractive foraging: The origins of imitation, teaching, and self-awareness in great apes. In *Reaching into thought: The minds of the great apes*, eds., Russon, A.E., Bard, K.A. and Parker, S.T.. Cambridge, Cambridge University Press, pp.348-370.

Parker, S.T. and Milbrath, C., 1994. Contributions of imitation and role-playing games to the construction of self in primates. In *Self-awareness in animals and humans: Developmental perspectives*, eds., Taylor Parker, S., Mitchell, R.W., Boccia, M.L.. Cambridge, Cambridge University Press, pp.108-128.

Parncutt, R., 2009. Prenatal and infant conditioning, the mother schema, and the origins of music and religion. *Musicae Scientiae*, *13*(2_suppl), pp.119-150.

Parrott, W.G. and Gleitman, H., 1989. Infants' expectations in play: The joy of peek-a-boo. *Cognition & Emotion*, *3*(4), pp.291-311.

Paskind, H.A., 1932. Effect of laughter on muscle tone. *Archives of Neurology & Psychiatry*, *28*(3), pp.623-628.

Pasztory, E., 1996. Aesthetics and pre-Columbian art. *RES: Anthropology and Aesthetics*, *29*(1), pp.318-325.

Patel, A.D., Gibson, E., Ratner, J., Besson, M. and Holcomb, P.J., 1998. Processing syntactic relations in language and music: An event-related potential study. *Journal of cognitive neuroscience*, *10*(6), pp.717-733.

Patterson, F.G. and Gordon, W., 2002. Twenty-seven years of Project Koko and Michael. In *All apes great and small,* eds., Galdikas, B., Erickson Briggs, N., Sheeran, L., Shapiro, G., Goodall, J.. Boston, Springer, pp. 165-176.

Paulos, J.A., 2008. *Mathematics and humor: A study of the logic of humor*. Chicago, University of Chicago Press.

Pearce, E., Launay, J. and Dunbar, R.I., 2015. The ice-breaker effect: singing mediates fast social bonding. *Open Science*, *2*(10), p.150221.

Pearce, E., Launay, J., van Duijn, M., Rotkirch, A., David-Barrett, T. and Dunbar, R.I., 2016. Singing together or apart: The effect of competitive and cooperative singing on social bonding within and between sub-groups of a university Fraternity. *Psychology of music*, *44*(6), pp.1255-1273.

Pearlstein, T., Howard, M., Salisbury, A. and Zlotnick, C., 2009. Postpartum depression. *American journal of obstetrics and gynecology*, *200*(4), pp.357-364.

Peirce, C.S., 1991. *Peirce on signs: Writings on semiotic*. Chapel Hill, North Carolina, UNC Press Books.

Pellegrini, A.D. and Smith, P.K. eds., 2005. *The nature of play: Great apes and humans*. London, Guilford Press.

Peretz, I., 2006. The nature of music from a biological perspective. *Cognition*, *100*(1), pp.1-32.

Peretz, I. and Coltheart, M., 2003. Modularity of music processing. *Nature neuroscience*, *6*(7), p.688.

Petitto, L.A. and Marentette, P.F., 1991. Babbling in the manual mode: Evidence for the ontogeny of language. *Science*, *251*(5000), p.1493.

Piaget, J., 1971. *Biology and knowledge: An essay on the relations between organic regulations and cognitive processes.* Chicago, University of Chicago Press.

Piaget, J., 2013. *Behaviour and evolution*. London, Routledge.

Piaget, J., Piaget, J. and Boring, I.E. 1952. *A history of psychology in autobiography (Vol. 4).* New York, Russell.

Piattelli-Palmarini, M., 1989. Evolution, selection and cognition: From “learning” to parameter setting in biology and in the study of language. *Cognition*, *31*(1), pp.1-44.

Pinto, B. and Riesch, H., 2017. Are audiences receptive to humour in popular science articles? An exploratory study using articles on environmental issues. *Journal of Science Communication*, *16*(4), pp.1-15.

Pien, D. and Rothbart, M.K., 1980. Incongruity humour, play, and self-regulation of arousal in young children. *Children's humour*, pp.1-26.

Peirce, C.S., 1932. The icon, index, and symbol. *Collected papers of Charles Sanders Peirce*, *2*, Cambridge, Ma., Belknap, pp.156-173.

Pike, A.W., Hoffmann, D.L., Garcia-Diez, M., Pettitt, P.B., Alcolea, J., De Balbin, R., González-Sainz, C., de las Heras, C., Lasheras, J.A., Montes, R. and Zilhao, J., 2012. U-series dating of Paleolithic art in 11 caves in Spain. *Science*, *336*(6087), pp.1409-1413.

Pinker, S., 1997. *How the mind works*. New York, Norton.

Pinker, S., 1999. How the mind works. *Annals of the New York Academy of Sciences*, *882*(1), pp.119-127.

Pinker, S., 2003. *The language instinct: How the mind creates language*. London, Penguin UK.

Pinker, S. and Bloom, P., 1990. Natural language and natural selection. *Behavioral and brain sciences*, *13*(4), pp.707-727.

Pinker, S. and Jackendoff, R., 2005(a). The faculty of language: what's special about it?. *Cognition*, *95*(2), pp.201-236.

Pinker, S. and Jackendoff, R., 2005(b). The nature of the language faculty and its implications for evolution of language (Reply to Fitch, Hauser, and Chomsky). *Cognition*, *97*(2), pp.211-225.

Pinto, B. and Riesch, H., 2017. Are audiences receptive to humour in popular science articles? An exploratory study using articles on environmental issues. *Journal of Science Communication*, *16*(4), p.A01.

Pizzini, F., 1991. Communication hierarchies in humour: gender differences in the obstetrical/gynaecological setting. *Discourse & Society*, *2*(4), pp.477-488.

Plato.,1974. *The Republic*. London, Penguin Books.

Plessner, H., 1970. *Laughing and crying: a study of the limits of human behavior*. Evanston, Il., Northwestern University Press.

Plomin, R., 2000. Behavioural genetics in the 21st century. *International Journal of Behavioral Development*, *24*(1), pp.30-34.

Plooij, F., 1979. How wild chimpanzee babies trigger the onset of mother-infant play—and what the mother makes of it1. *Before speech: The beginning of interpersonal communication*, p.223.

Plutchik, R., 1982. *A psychoevolutionary theory of emotions,* Social Science Information, Volume: 21 issue: 4-5, , Issue published: July 1, 1982, pp. 529-553.

Pogue-Geile, M., Ferrell, R., Deka, R., Debski, T. and Manuck, S., 1998. Human novelty-seeking personality traits and dopamine D4 receptor polymorphisms: a twin and genetic association study. *American Journal of Medical Genetics Part A*, *81*(1), pp.44-48.

Polimeni, J. and Reiss, J.P., 2006. The first joke: Exploring the evolutionary origins of humor. *Evolutionary Psychology*, *4*(1), p.147470490600400129.

Pollick, A.S. and De Waal, F.B., 2007. Ape gestures and language evolution. *Proceedings of the National Academy of Sciences*, *104*(19), pp.8184-8189.

Pollio, H.R., Mers, R. and Lucchesi, W., 1972. Humor, laughter, and smiling: Some preliminary observations of funny behaviors. *The psychology of humor*, pp.211-239.

Popper, K., 2005. *The logic of scientific discovery*. London, Routledge.

Porteous, J., 1989. Humor and social life. *Philosophy East and West*, *39*(3), pp.279-288.

Potter, R.E. and Goodman, N.J., 1983. The implementation of laughter as a therapy facilitator with adult aphasics. *Journal of communication disorders*, *16*(1), pp.41-48.

Poyatos, F. ed., 1992. *Advances in Non-Verbal Communication: Sociocultural, clinical, esthetic and literary perspectives*. Philadelphia, John Benjamins Publishing Company.

Premack, D., 1971. Language in chimpanzee. *Science*, *172*(3985), pp.808-822.

Premack, D. and Woodruff, G., 1978. Does the chimpanzee have a theory of mind?. *Behavioral and brain sciences*, *1*(4), pp.515-526.

Preuschoft, S., 1992. “Laughter” and “smile” in Barbary macaques (Macaca sylvanus). *Ethology*, *91*(3), pp.220-236.

Preuschoft, S. and Beckmann, F., 1995. ‘Smiling’ and ‘laughter’ in lion-tailed macaques (Macaca silenus): a preliminary analysis of their bared-teeth displays. *Laughter’and ‘Smiling’in Macaques. An Evolutionary Perspective (Preuschoft S, doctoral dissertation)*, pp.111-136.

Preuschoft, S. and van Hooff, J.A., 1997. The social function of "smile" and "laughter": Variations across primate species and societies. In *Nonverbal communication: Where nature meets culture*, eds., Segerstråle, U.C., and Molnár, P.. Hillsdale, NJ, US: Lawrence Erlbaum Associates, Inc., pp. 171-190.

Previc, F.H., 1999. Dopamine and the origins of human intelligence. *Brain and cognition*, *41*(3), pp.299-350.

Price, E. O., 1984: Behavioral aspects of animal domestication. *Qu. Rev. Biol. 59*.

Price, T.D., Qvarnström, A. and Irwin, D.E., 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*(1523), pp.1433-1440.

Prkachin, K.M. and Silverman, B.E., 2002. Hostility and facial expression in young men and women: Is social regulation more important than negative affect?. *Health Psychology*, *21*(1), p.33.

Provine, R.R., 1992. Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. *Bulletin of the Psychonomic Society*, *30*(1), pp.1-4.

Provine, R.R., 1993. Laughter punctuates speech: Linguistic, social and gender contexts of laughter. *Ethology*, *95*(4), pp.291-298.

Provine, R.R., 1996. Laughter. *American scientist*, *84*(1), pp.38-45.

Provine, R.R., 2001. *Laughter: A scientific investigation*. New York, Penguin.

Provine, R.R., 2004. Laughing, tickling, and the evolution of speech and self. *Current Directions in Psychological Science*, *13*(6), pp.215-218.

Provine, R.R., 2016. Laughter as a scientific problem: An adventure in sidewalk neuroscience. *Journal of Comparative Neurology*, *524*(8), pp.1532-1539.

Provine, R. R., & Fischer, K. R. (1989). Laughing, smiling, and talking: Relation to sleeping and social context in humans. Ethology, 83(4), 295-305.

Puts, D.A., 2010. Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, *31*(3), pp.157-175.

Radcliffe-Brown, A.R., 1940. On joking relationships. *Africa*, *13*(3), pp.195-210.

Raghanti, M.A., Edler, M.K., Stephenson, A.R., Wilson, L.J., Hopkins, W.D., Ely, J.J., Erwin, J.M., Jacobs, B., Hof, P.R. and Sherwood, C.C., 2016. Human-specific increase of dopaminergic innervation in a striatal region associated with speech and language: A comparative analysis of the primate basal ganglia. *Journal of Comparative Neurology*, *524*(10), pp.2117-2129.

Ramachandran, V.S., 1998. The neurology and evolution of humor, laughter, and smiling: the false alarm theory. *Medical hypotheses*, *51*(4), pp.351-354.

Ramachandran, V.S., 2000. Mirror neurons and imitation learning as the driving force behind “the great leap forward” in human evolution. Online source: http://www.edge.org/3rd_culture/

Ramsey, J.K. and McGrew, W.C., 2005. Object play in great apes. In *The nature of play: Great apes and humans*, eds., Pellegrini, A.D. and Smith, P.K.. London, Guilford Press, pp.89-112.
Range, F., Huber, L. and Heyes, C., 2011. Automatic imitation in dogs. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1703), pp.211-217.

Raskin, V., 2012. *Semantic mechanisms of humor* (Vol. 24). New York, Springer Science & Business Media.

Reader, S.M., Kendal, J.R. and Laland, K.N., 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, *66*(4), pp.729-739.

Reader, S.M. and Laland, K.N., 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), pp.4436-4441.

Reddy, V., 1998. Person-directed play: Humour and teasing in infants and young children. *Report on Grant*, (R000235481).

Reddy, V., 2001. Infant clowns: The interpersonal creation of humour in infancy. *Enfance*, *53*(3), pp.247-256.

Reddy, V., 2008. *How infants know minds*. Cambridge, Ma., Harvard University Press.

Reeve, H.K. and Sherman, P.W., 1993. Adaptation and the goals of evolutionary research. *The Quarterly Review of Biology*, *68*(1), pp.1-32.

Reilly, J.S., McIntire, M. and Bellugi, U., 1990. The acquisition of conditionals in American Sign Language: Grammaticized facial expressions. *Applied Psycholinguistics*, *11*(4), pp.369-392.

Reinhart, T., 1984. Principles of gestalt perception in the temporal organization of narrative texts. *Linguistics*, *22*(6), pp.779-810.

Richards, R.J., 1989. Darwin and the emergence of evolutionary theories of mind and behavior. Chicago, University of Chicago Press.

Richerson, P.J. and Boyd, R., 2010. Why possibly language evolved. *Biolinguistics*, *4*(2-3), pp.289-306.

Riem, M.M., Van Ijzendoorn, M.H., Tops, M., Boksem, M.A., Rombouts, S.A. and Bakermans-Kranenburg, M.J., 2012. No laughing matter: intranasal oxytocin administration changes functional brain connectivity during exposure to infant laughter. *Neuropsychopharmacology*, *37*(5), p.1257.

Rifkin, R.F., d'Errico, F., Dayet-Boulliot, L. and Summers, B., 2015. Assessing the photoprotective effects of red ochre on human skin by in vitro laboratory experiments. *South African Journal of Science*, *111*(3-4), pp.1-8.

Rimé, B., 2007. The social sharing of emotion as an interface between individual and collective processes in the construction of emotional climates. *Journal of social issues*, *63*(2), pp.307-322.

Rimé, B., 2009. Emotion elicits the social sharing of emotion: Theory and empirical review. *Emotion review*, *1*(1), pp.60-85.

Ritchie, G., 1999. *Developing the incongruity-resolution theory*. Division of Informatics, University of Edinburgh.

Robinson, D.L. and Petersen, S.E., 1992. The pulvinar and visual salience. *Trends in neurosciences*, *15*(4), pp.127-132.

Roebroeks, W., Sier, M.J., Nielsen, T.K., De Loecker, D., Parés, J.M., Arps, C.E. and Mücher, H.J., 2012. Use of red ochre by early Neandertals. *Proceedings of the National Academy of Sciences*, *109*(6), pp.1889-1894.

Rogers, S.J., Hepburn, S.L., Stackhouse, T. and Wehner, E., 2003. Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of child psychology and psychiatry*, *44*(5), pp.763-781.

Rolls, E.T., 1990. A theory of emotion, and its application to understanding the neural basis of emotion. *Cognition & Emotion*, *4*(3), pp.161-190.

Rolls, E.T., 2000. On the brain and emotion. *Behavioral and brain sciences*, *23*(2), pp.219-228.

Rolls, E.T., 2011. A neurobiological basis for affective feelings and aesthetics. In *The Aesthetic Mind: Philosophy and Psychology*, eds., Schellekens, E., and Goldie, P.. Oxford, Oxford University Press, pp. 116-165.

Rolls, E.T., 2013. A biased activation theory of the cognitive and attentional modulation of emotion. *Frontiers in human neuroscience*, *7*.

Rolls, E.T., 2013. *Emotion and decision making explained*. Oxford, Oxford University Press.

Rolls, E.T., 2017. Neurobiological foundations of aesthetics and art. *New Ideas in Psychology*, *47*, pp.121-135.

Romero, E. and Pescosolido, A., 2008. Humor and group effectiveness. *Human Relations*, *61*(3), pp.395-418.

Rosario, J. and Collazo, E., 1981. Aesthetic codes in context: An exploration in two preschool classrooms. *Journal of Aesthetic Education*, *15*(1), pp.71-82.

Ross, M.D., Owren, M.J. and Zimmermann, E., 2009. Reconstructing the evolution of laughter in great apes and humans. *Current Biology*, *19*(13), pp.1106-1111.

Ross, M.D., Owren, M.J. and Zimmermann, E., 2010. The evolution of laughter in great apes and humans. *Communicative & integrative biology*, *3*(2), pp.191-194.

Rothbart, M.K., 1973. Laughter in young children. *Psychological bulletin*, *80*(3), p.247.

Rothbart, M.K., 1977. Psychological approaches to the study of humour.In *It's a funny thing, Humour*, eds., Chapman, A.J. and Foot, H.C. New York, Elsevier, pp.87-94.

Rothbart, M.K. and Pien, D., 1977. *Elephants and marshmallows: A theoretical synthesis of incongruity-resolution and arousal theories of humour* (pp. 37-40). Oxford, Pergamon Press.

Rothenberg, D., Roeske, T.C., Voss, H.U., Naguib, M. and Tchernichovski, O., 2014. Investigation of musicality in birdsong. *Hearing research*, *308*, pp.71-83.

Routhieaux, R.L. and Tansik, D.A., 1997. The benefits of music in hospital waiting rooms. *The Health care supervisor*, *16*(2), pp.31-40.

Ruch, W., 1988. Sensation seeking and the enjoyment of structure and content of humour: Stability of findings across four samples. *Personality and Individual Differences*, *9*(5), pp.861-871.

Ruch, W., 1993. Exhilaration and humor. In *Handbook of emotions*, *1*, eds., Lewis, M., Haviland-Jones, J., Feldman-Barrett, L.. London, Guilford Press pp.605-616.

Ruch, W., 1995. Will the real relationship between facial expression and affective experience please stand up: The case of exhilaration. *Cognition & Emotion*, *9*(1), pp.33-58.

Ruch, W. and Deckers, L., 1993. 'Do extraverts like to laugh'?: An analysis of the Situational Humor Response Questionnaire (SHRQ). *European Journal of Personality*, *7*(4), pp.211-220.

Ruch, W. and Köhler, G., 1998. A temperament approach to humor. In *The sense of humor: Explorations of a personality characteristic,* ed., Ruch, W.. London, Walter de Gruyter, pp.203-230.

Ruch, W., Köhler, G. and Van Thriel, C., 1996. Assessing the „humorous temperament ": Construction of the facet and standard trait forms of the State-Trait-Cheerfulness-Inventory—STCI. *Humor-International Journal of Humor Research*, *9*(3-4), pp.303-340.

Rumbaugh, D.M. ed., 2014. *Language learning by a chimpanzee: The Lana project*. New York, Academic Press.

Rumbaugh, D.M. and Gill, T.V., 1973. The learning skills of great apes. *Journal of Human Evolution*, *2*(3), pp.171-179.

Rumelhart, D., 1980. Schemata: The building blocks of cognition. In *Theoretical issues in reading comprehension,* eds., Spiro, R., Bruce, B., and Brewer., W. Hillsdale, Routledge.

Russell, J.A., 1994. Is there universal recognition of emotion from facial expression? A review of the cross-cultural studies. *Psychological bulletin*, *115*(1), p.102.

Rust, J. and Goldstein, J., 1989. Humor in marital adjustment. *Humor-International Journal of Humor Research*, *2*(3), pp.217-224.

Rutter, J., 2001. Rhetoric in stand-up comedy: Exploring performer-audience interaction. *Stylistyka*, *10*, pp.307-325.

Rygula, R., Pluta, H. and Popik, P., 2012. Laughing rats are optimistic. *PLoS One*, *7*(12), p.e51959.

Sabar, S., 2013. What's a Gestalt?. *Gestalt Review*, *17*(1).

Sadalla, E.K., Kenrick, D.T. and Vershure, B., 1987. Dominance and heterosexual attraction. *Journal of Personality and Social Psychology*, *52*(4), p.730.

Sagi, I. and Yechiam, E., 2008. Amusing titles in scientific journals and article citation. *Journal of Information Science*, *34*(5), pp.680-687.

Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A. and Zatorre, R.J., 2013. Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science*, *340*(6129), pp.216-219.

Salimpoor, V.N., Benovoy, M., Larcher, K., Dagher, A. and Zatorre, R.J., 2011. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature neuroscience*, *14*(2), pp.257-262.

Salovey, P., Rothman, A.J., Detweiler, J.B. and Steward, W.T., 2000. Emotional states and physical health. *American psychologist*, *55*(1), p.110.

Samson, A.C., Huber, O. and Ruch, W., 2013. Seven decades after Hans Asperger's observations: A comprehensive study of humor in individuals with Autism Spectrum Disorders. *Humor – Internation Journal of Humor Research*, *26*(3), pp.441-460.

Samuels, R., 2000. Massively modular minds: Evolutionary psychology and cognitive architecture. In *Evolution and the human mind: Modularity, language and meta-cognition*, eds. Carruthers, P. and Chamberlain, A.. Cambridge, Cambridge University Press, pp.13-46.

Sandblom, P., 1992. *Creativity and disease: How illness affects literature, art and music*. New York, Marion Boyars.

Saragusti, I., Sharon, I., Katzenelson, O. and Avnir, D., 1998. Quantitative analysis of the symmetry of artefacts: Lower Paleolithic handaxes. *Journal of Archaeological Science*, *25*(8), pp.817-825.

Saroglou, V. and Scariot, C., 2002. Humor Styles Questionnaire: Personality and educational correlates in Belgian high school and college students. *European Journal of Personality*, *16*(1), pp.43-54.

Sasaki, J.Y., Kim, H.S., Mojaverian, T., Kelley, L.D., Park, I.Y. and Janušonis, S., 2011. Religion priming differentially increases prosocial behavior among variants of the dopamine D4 receptor (DRD4) gene. *Social Cognitive and Affective Neuroscience*, *8*(2), pp.209-215.

Savage-Rumbaugh, E.S., Sevcik, R.A., Rumbaugh, D.M. and Rubert, E., 1985. The capacity of animals to acquire language: do species differences have anything to say to us?. *Phil. Trans. R. Soc. Lond. B*, *308*(1135), pp.177-185.

Savage-Rumbaugh, S., Rumbaugh, D.M. and McDonald, K., 1985. Language learning in two species of apes. *Neuroscience & Biobehavioral Reviews*, *9*(4), pp.653-665.

Schachter, S. and Wheeler, L., 1962. Epinephrine, chlorpromazine, and amusement. *The Journal of Abnormal and Social Psychology*, *65*(2), p.121.

Scheerer, M., 1966. An aspect of the psychology of humor. *Bulletin of the Menninger Clinic*, *30*(2), p.86.

Scheiner, E., Hammerschmidt, K., Jürgens, U. and Zwirner, P., 2006. Vocal expression of emotions in normally hearing and hearing-impaired infants. *Journal of Voice*, *20*(4), pp.585-604.

Scherer, K.R., 1994. Affect bursts. In *Emotions: Essays on emotion theory*, eds.,Van Goozen, S.H., Van de Poll, N.E., Sergeant, J.A., Sergeant, J.A. and Van Goozen, S.H.M.. New York, Psychology Press, p.196.

Schilbach, L., Wohlschlaeger, A. M., Kraemer, N. C., Newen, A., Shah, N. J., Fink, G. R., & Vogeley, K., 2006. Being with virtual others: Neural correlates of social interaction. *Neuropsychologia*, *44*(5), 718-730.

Schmitt, D.P. and Buss, D.M., 2000. Sexual dimensions of person description: beyond or subsumed by the Big Five?. *Journal of Research in Personality*, *34*(2), pp.141-177.

Schmidt, K.L. and Cohn, J.F., 2001. Human facial expressions as adaptations: Evolutionary questions in facial expression research. *American journal of physical anthropology*, *116*(S33), pp.3-24.

Schmidt, S.R., 1994. Effects of humor on sentence memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*(4), p.953.

Schmidt, S.R., 2002. The humour effect: Differential processing and privileged retrieval. *Memory*, *10*(2), pp.127-138.

Schnurr, S., 2009. Constructing leader identities through teasing at work. *Journal of Pragmatics*, *41*(6), pp.1125-1138.

Schopenhauer, A., 1966. *The World as Will and Representation, Volume 2*, New York, Dover.

Schott, B.H., Sellner, D.B., Lauer, C.J., Habib, R., Frey, J.U., Guderian, S., Heinze, H.J. and Düzel, E., 2004. Activation of midbrain structures by associative novelty and the formation of explicit memory in humans. *Learning & Memory*, *11*(4), pp.383-387.

Schwartz, S., Ponz, A., Poryazova, R., Werth, E., Boesiger, P., Khatami, R. and Bassetti, C.L., 2007. Abnormal activity in hypothalamus and amygdala during humour processing in human narcolepsy with cataplexy. *Brain*, *131*(2), pp.514-522.

Scott, E. and Panksepp, J., 2003. Rough-and-tumble play in human children. *Aggressive behavior*, *29*(6), pp.539-551.

Scruton, R., and Jones, P.,1982. Laughter. *Proceedings of the Aristotelian Society, Supplementary Volumes, 56*, 197-228.

Seaman, M.I., Fisher, J.B., Chang, F.M. and Kidd, K.K., 1999. Tandem duplication polymorphism upstream of the dopamine D4 receptor gene (DRD4). *American journal of medical genetics*, *88*(6), pp.705-709.

Selden, S.T., 2004. Tickle. *Journal of the American Academy of Dermatology*, *50*(1), pp.93-97.

Selye, H., 1956. *The stress of life*. New York, Mcgraw Hill.

Semrud-Clikeman, M. and Glass, K., 2010. The relation of humor and child development: Social, adaptive, and emotional aspects. *Journal of child neurology*, *25*(10), pp.1248-1260.

Seyfarth, R.M., Cheney, D.L. and Bergman, T.J., 2005. Primate social cognition and the origins of language. *Trends in cognitive sciences*, *9*(6), pp.264-266.

Seyfarth, R.M., Cheney, D.L. and Marler, P., 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, *210*(4471), pp.801-803.

Shammi, P. and Stuss, D.T., 1999. Humour appreciation: a role of the right frontal lobe. *Brain*, *122*(4), pp.657-666.

Sharpe, S., Dewsbury, J.D. and Hynes, M., 2014. The Minute Interventions of Stewart Lee: The affirmative conditions of possibility in comedy, repetition and affect. *Performance Research*, *19*(2), pp.116-125.

Shatz, C.J., 1990. Impulse activity and the patterning of connections during CNS development. *Neuron*, *5*(6), pp.745-756.

Shea, B.T., 1989. Heterochrony in human evolution: the case for neoteny reconsidered. *American Journal of Physical Anthropology*, *32*(S10), pp.69-101.

Sherman, K.M., 1998, April. Healing with humor. In *Seminars in perioperative nursing*. Vol. 7, No. 2, pp. 128-137.

Shimada, M., 2013. Wild chimpanzees can perform social grooming and social play behaviors simultaneously. *Primates*, *54*(4), pp.315-317.

Shultz, T.R., 1976. A cognitive-developmental analysis of humour. In *Humor and laughter: Theory, research, and applications,* eds., Chapman, A.J., and Foot, H.C.. Piscataway, NJ, Transaction Publishers, pp.11-36.

Silk, J.B., 2002. Grunts, girneys, and good intentions: The origins of strategic commitment in nonhuman primates. *Evolution and the capacity for commitment*, *3*, pp.138-157.

Silvia, P.J., Winterstein, B.P., Willse, J.T., Barona, C.M., Cram, J.T., Hess, K.I., Martinez, J.L. and Richard, C.A., 2008. Assessing creativity with divergent thinking tasks: Exploring the reliability and validity of new subjective scoring methods. *Psychology of Aesthetics, Creativity, and the Arts*, *2*(2), p.68.

Simonet, P., Murphy, M. and Lance, A., 2001, July. Laughing dog: Vocalizations of domestic dogs during play encounters. In *Animal Behavior Society Conference,* pp. 14-18.

Simonet, P., Versteeg, D. and Storie, D., 2005, July. Dog-laughter: Recorded playback reduces stress related behavior in shelter dogs. In *Proceedings of the 7th International Conference on Environmental Enrichment* (Vol. 2005).

Simonyan, K., Horwitz, B. and Jarvis, E.D., 2012. Dopamine regulation of human speech and bird song: a critical review. *Brain and language*, *122*(3), pp.142-150.

Singer, D.L., 1968. Aggression arousal, hostile humor, catharsis. *Journal of Personality and Social Psychology*, *8*(1p2), p.1.

Slobin, D.I., 2004. From ontogenesis to phylogenesis: What can child language tell us about language evolution. In *Biology and knowledge revisited: From neurogenesis to psychogenesis*, eds., Parker, S.T., Langer, J. and Milbrath, C.. Mahwah N.J., Psychology Press, pp.255-286.

Smith, B.H. and Tompkins, R.L., 1995. Toward a life history of the Hominidae. *Annual Review of Anthropology*, *24*(1), pp.257-279.

Smith, T.M., Tafforeau, P., Reid, D.J., Grün, R., Eggins, S., Boutakiout, M. and Hublin, J.J., 2007. Earliest evidence of modern human life history in North African early Homo sapiens. *Proceedings of the National Academy of Sciences*, *104*(15), pp.6128-6133.

Smith, T.M., Toussaint, M., Reid, D.J., Olejniczak, A.J. and Hublin, J.J., 2007. Rapid dental development in a middle Paleolithic Belgian Neanderthal. *Proceedings of the National Academy of Sciences*, *104*(51), pp.20220-20225.

Smolensky, P., 1988. *Connectionism, constituency, and the language of thought*. Boulder, Co, University of Colorado at Boulder.

Smoski, M. and Bachorowski, J.A., 2003. Antiphonal laughter between friends and strangers. *Cognition & Emotion*, *17*(2), pp.327-340.

Snell, J., 2006. Schema theory and the humour of Little Britain. *English Today*, *22*(1), pp.59-64.

Snetsinger, W. and Grabowski, B., 1993. Use of Humorous Visuals To Enhance Computer-Based-Instruction. In *Visual Literacy in the Digital Age: Selected Readings from the Annual Conference of the International Visual Literacy Association* (25th, Rochester, New York, October 13-17, 1993.

Soderstrom, M., 2007. Beyond babytalk: Re-evaluating the nature and content of speech input to preverbal infants. *Developmental Review*, *27*(4), pp.501-532.

Sohr-Preston, S.L. and Scaramella, L.V., 2006. Implications of timing of maternal depressive symptoms for early cognitive and language development. *Clinical child and family psychology review*, *9*(1), pp.65-83.

Spencer, H., 1860. *The physiology of laughter*. New York, Macmillan.

Sperber, D., 2001. In defense of massive modularity. *Language, brain and cognitive development: Essays in honor of Jacques Mehler*, *47*.

Sperber, D., 2017. *Personal correspondence*. E-mail, November 22nd, 2017.

Spielman, D., Brook, B.W., Briscoe, D.A. and Frankham, R., 2004. Does inbreeding and loss of genetic diversity decrease disease resistance?. *Conservation Genetics*, *5*(4), pp.439-448.

Sprecher, S. and Regan, P.C., 2002. Liking some things (in some people) more than others: Partner preferences in romantic relationships and friendships. *Journal of Social and Personal Relationships*, *19*(4), pp.463-481.

Srofe, L.A. and Waters, E., 1976. The ontogenesis of smiling and laughter: a perspective on the organization of development in infancy. *Psychological review*, *83*(3), p.173.

Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist*, *98*(1), pp.96-113.

Stanley, H.M., 1898. Remarks on tickling and laughing. *The American Journal of Psychology*, *9*(2), pp.235-240.

Stebbins, R.A., 1996. Defusing awkward situations: comic relief as an interactive strategy for people with disabilities. *Journal of Leisurability*, *23*(4), pp.3-38.

Sterelny, K., 2007. Social intelligence, human intelligence and niche construction. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1480), pp.719-730.

Stevens, J., 2012. Stand up for dementia: Performance, improvisation and stand up comedy as therapy for people with dementia; a qualitative study. *Dementia*, *11*(1), pp.61-73.

Stokoe Jr, W.C., 2005. Sign language structure: An outline of the visual communication systems of the American deaf. *Journal of deaf studies and deaf education*, *10*(1), pp.3-37.

Storbeck, J. and Clore, G.L., 2005. With sadness comes accuracy; with happiness, false memory: Mood and the false memory effect. *Psychological Science*, *16*(10), pp.785-791.

Strapparava, C., Stock, O. and Mihalcea, R., 2011. Computational humour. In *Emotion-oriented systems*. Berlin Heidelberg, Springer, pp. 609-634

Stuckey, H.L. and Nobel, J., 2010. The connection between art, healing, and public health: A review of current literature. *American journal of public health*, *100*(2), pp.254-263.

Studdert-Kennedy, M. and Goldstein, L., 2003. Launching language: The gestural origin of discrete infinity. *Studies in the Evolution of Language*, *3*, pp.235-254.

Styan, J.L., 1968. *The dark comedy* (Vol. 529). Cambridge, Cambridge University Press.

Sugawara, J., Tarumi, T. and Tanaka, H., 2010. Effect of mirthful laughter on vascular function. *The American journal of cardiology*, *106*(6), pp.856-859.

Sullivan, K., Winner, E. and Hopfield, N., 1995. How children tell a lie from a joke: The role of second-order mental state attributions. *British Journal of Developmental Psychology*, *13*(2), pp.191-204.

Sully, J., 1902. *An essay on laughter: Its forms, its causes, its development and its value*. London, Longmans, Green, and Company.

Suls, J.M., 1972. A two-stage model for the appreciation of jokes and cartoons: An information-processing analysis. *The psychology of humor: Theoretical perspectives and empirical issues*, *1*, pp.81-100.

Summerfelt, H., Lippman, L. and Hyman Jr, I.E. 2010. The effect of humor on memory: Constrained by the pun. *The Journal of General Psychology*, *137*(4), pp.376-394.

Suslov, I.M., 1992. Computer model of a sense of humour I. General Algorithm. *Biophysics*, *37*(2), pp.242-248.

Susman, R.L., 1994. Fossil evidence for early hominid tool use. *Science*, *265*(5178), pp.1570-1574

Svebak, S., 1982. The effect of mirthfulness upon amount of discordant right-left occipital EEG alpha. *Motivation and emotion*, *6*(2), pp.133-147.

Szameitat, D.P., Kreifelts, B., Alter, K., Szameitat, A.J., Sterr, A., Grodd, W. and Wildgruber, D., 2010. It is not always tickling: distinct cerebral responses during perception of different laughter types. *Neuroimage*, *53*(4), pp.1264-1271.

Taglialatela, J.P., Reamer, L., Schapiro, S.J. and Hopkins, W.D., 2012. Social learning of a communicative signal in captive chimpanzees. *Biology Letters*, *8*(4), pp.498-501.

Taglialatela, J.P., Savage-Rumbaugh, S. and Baker, L.A., 2003. Vocal production by a language-competent Pan paniscus. *International Journal of Primatology*, *24*(1), pp.1-17.

Tajfel, H. and Turner, J.C., 1979. An integrative theory of intergroup conflict. *The social psychology of intergroup relations*, *33*(47), p.74.

Tajfel, H. and Turner, J.C., 2004. The Social Identity Theory of Intergroup Behavior. In J. T. Jost & J. Sidanius (Eds.), *Key readings in social psychology. Political psychology: Key readings* (pp. 276-293). New York, NY, US: Psychology Press.

Takahashi, K. and Watanabe, K., 2013. Gaze cueing by pareidolia faces. *i-Perception*, *4*(8), pp.490-492.

Talarico, J.M., Berntsen, D. and Rubin, D.C., 2009. Positive emotions enhance recall of peripheral details. *Cognition and Emotion*, *23*(2), pp.380-398.

Tan, S.A., Tan, L.G., Lukman, S.T. and Berk, L.S., 2007. Humor, as an adjunct therapy in cardiac rehabilitation, attenuates catecholamines and myocardial infarction recurrence. *Advances in mind-body medicine*, *22*(3-4), pp.8-12.

Tannen, D., 2001. Sex, Lies and Conversation: Why is it so Hard for Men and Women to Talk to Each Other?. In *Conflict, Order and Action: Readings in Sociology*, eds., Ksenych, E. and Liu, D.. Toronto, Canadian Scholars' Press, pp.244-248.

Tanner, J.E. and Byrne, R.W., 2010. Triadic and collaborative play by gorillas in social games with objects. *Animal cognition*, *13*(4), pp.591-607.

Tattersall, I., 1995. *The fossil trail: How we know what we think we know about human evolution*. Oxford, Oxford University Press, USA.

Taubert, J., Wardle, S.G., Flessert, M., Leopold, D.A. and Ungerleider, L.G., 2017. Face pareidolia in the rhesus monkey. *Current Biology*, *27*(16), pp.2505-2509.

Taylor, H., 2017. *Is Birdsong Music?: Outback Encounters with an Australian Songbird*. Bloomington, Indiana University Press.

Teh, Y.W., 2006, July. A hierarchical Bayesian language model based on Pitman-Yor processes. In *Proceedings of the 21st International Conference on Computational Linguistics and the 44th annual meeting of the Association for Computational Linguistics*. Association for Computational Linguistics, pp. 985-992.

Tennie, C., Call, J. and Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1528), pp.2405-2415.

Thompson, K.G. and Bichot, N.P., 2005. A visual salience map in the primate frontal eye field. *Progress in brain research*, *147*, pp.249-262.

Thorpe, W., 1963. *Learning and instinct in animals*. London, Methuen.

Tinbergen, N., 1963. On aims and methods of ethology. *Ethology*, *20*(4), pp.410-433.

Tishkoff, S.A. and Verrelli, B.C., 2003. Patterns of human genetic diversity: implications for human evolutionary history and disease. *Annual review of genomics and human genetics*, *4*(1), pp.293-340.

Tolstoy, L., 1995. *What is art?*. London, Penguin UK.

Tomasello, M., 1994. 10 Cultural transmission in the tool use and communicatory signaling of chimpanzees?. *'Language'and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*, p.274.

Tomasello, M., 1995. Joint attention as social cognition. In *Joint attention: Its origins and role in development*, eds., Moore, C., Dunham, P.J. and Dunham, P.. New York, Psychology Press, p.*103130*.

Tomasello, M., 1996. Do apes ape. In *Social learning in animals: The roots of culture*, eds. Heyes, C.M. and Galef Jr, B.G.. San Diego, Academic Press, pp.319-346.

Tomasello, M., 2003. On the different origins of symbols and grammar. In Language Evolution, eds., Christiansen, M.H. and Kirby, S. Oxford, Oxford University Press. pp.94-110.

Tomasello, M., 2009. *The cultural origins of human cognition*. Cambridge, Ma., Harvard University Press.

Tomasello, M. and Call, J., 1997. *Primate cognition*. New York, Oxford University Press, USA.

Tomasello, M., Call, J. and Gluckman, A., 1997. Comprehension of novel communicative signs by apes and human children. *Child development*, *68*(6), pp.1067-1080.

Tomasello, M. and Carpenter, M., 2007. Shared intentionality. *Developmental science*, *10*(1), pp.121-125.

Tomasello, M., Carpenter, M., Call, J., Behne, T. and Moll, H., 2005. In search of the uniquely human. *Behavioral and brain sciences*, *28*(5), pp.721-727.

Tomasello, M., and Farrar, J., 1986. Joint attention and early language*. Child Development, 57*, pp.1454-1463

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M.A.S.A.K.O., Kosugi, D., Mizuno, Y., Okamoto, S., Yamaguchi, M.K. and Bard, K.A., 2004. Development of social cognition in infant chimpanzees (Pan troglodytes): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research*, *46*(3), pp.227-235.

Toth, N. and Schick, K., 1993. Early stone industries and inferences regarding language and cognition. *Tools, language and cognition in human evolution*, pp.346-362.

Trainor, L.J. and Corrigall, K.A., 2010. Music acquisition and effects of musical experience. In *Music perception – Springer Handbook of Auditory Research, vol. 36,* eds., Riess Jones, M., Fay, R., Popper, A.. New York, Springer, pp. 89-127.

Trainor, L.J., Marie, C., Gerry, D., Whiskin, E. and Unrau, A., 2012. Becoming musically enculturated: effects of music classes for infants on brain and behavior. *Annals of the New York Academy of Sciences*, *1252*(1), pp.129-138.

Treisman, A.M. and Gelade, G., 1980. A feature-integration theory of attention. *Cognitive psychology*, *12*(1), pp.97-136.

Trovik, Ginger L., 2010. *Upper Paleolithic Art: a Creative Teaching tool*. All Regis University Theses. Paper 461.

Tse, D., Langston, R.F., Kakeyama, M., Bethus, I., Spooner, P.A., Wood, E.R., Witter, M.P. and Morris, R.G., 2007. Schemas and memory consolidation. *Science*, *316*(5821), pp.76-82.

Tsoi, D.Y., Lee, K.H., Gee, K.A., Holden, K.L., Parks, R.W. and Woodruff, P.W., 2008. Humour experience in schizophrenia: relationship with executive dysfunction and psychosocial impairment. *Psychological medicine*, *38*(6), pp.801-810.

Tulving, E., 1985. How many memory systems are there?. *American psychologist*, *40*(4), p.385.

Tulving, E., Markowitsch, H.J., Craik, F.I., Habib, R. and Houle, S., 1996. Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cerebral Cortex*, *6*(1), pp.71-79.

Tylor, E.B., 1871. *Primitive culture: researches into the development of mythology, philosophy, religion, art, and custom* (Vol. 2). London, J. Murray.

Uvnäs-Moberg, K., 1998. Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology*, *23*(8), pp.819-835.

Vaid, J. and Ramachandran, V.S., 2001. Laughter and humour, from Blakemore, C. and Jennett, S. eds., 2001. *The Oxford companion to the body* (Vol. 7). New York, Oxford University Press. P. 426.

Valdesolo, P., Ouyang, J. and DeSteno, D., 2010. The rhythm of joint action: Synchrony promotes cooperative ability. *Journal of Experimental Social Psychology*, *46*(4), pp.693-695.

Valerio, W.H., Seaman, M.A., Yap, C.C., Santucci, P.M. and Tu, M., 2006. Vocal evidence of toddler music syntax acquisition: A case study. *Bulletin of the Council for Research in Music Education*, pp.33-45.

Valli, C. and Lucas, C., 2000. *Linguistics of American sign language: An introduction*. Washington, Gallaudet University Press.

van de Waal, E., Borgeaud, C. and Whiten, A., 2013. Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), pp.483-485.

Van der Lely, H.K., 1997. Language and cognitive development in a grammatical SLI boy: Modularity and innateness. *Journal of Neurolinguistics*, *10*(2), pp.75-107.

van Hooff, J.A., 1972. A comparative approach to the phylogeny of laughter and smiling. In *Non-verbal communication, ed. Hinde, R.A.*. Oxford, Cambridge University Press.

van Hooff, J.A., and Preuschoft, S.,2003. Laughter and smiling: The intertwining of nature and culture. In *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, eds., F.B.M. de Waal and P.L. Tyack, Cambridge, Ma., Harvard University Press, pp. 260–287.

van Kesteren, M.T., Ruiter, D.J., Fernández, G. and Henson, R.N., 2012. How schema and novelty augment memory formation. *Trends in neurosciences*, *35*(4), pp.211-219.

Van Vugt, M., Hardy, C., Stow, J. and Dunbar, R., 2014. Laughter as social lubricant: a biosocial hypothesis about the pro-social functions of laughter and humor. *Centre for the Study of Group Processes Working Paper, University of Kent*.

Vauclair, J. and Bard, K.A., 1983. Development of manipulations with objects in ape and human infants. *Journal of Human Evolution*, *12*(7), pp.631-645.

Veatch, T., 2009. A theory of humor. *Humor - International Journal of Humor Research*, 11(2), pp. 161-216.

Vernon, P.A., Martin, R.A., Schermer, J.A. and Mackie, A., 2008. A behavioral genetic investigation of humor styles and their correlations with the Big-5 personality dimensions. *Personality and Individual Differences*, *44*(5), pp.1116-1125.

Viana, A., 2017. Humour and laughter as vestiges of evolution. *The European Journal of Humour Research*, *5*(1), pp.1-18.

Vilà, C., Savolainen, P., Maldonado, J.E., Amorim, I.R., Rice, J.E., Honeycutt, R.L., Crandall, K.A., Lundeberg, J. and Wayne, R.K., 1997. Multiple and ancient origins of the domestic dog. *Science*, *276*(5319), pp.1687-1689.

Vlachopoulos, C., Xaplanteris, P., Alexopoulos, N., Aznaouridis, K., Vasiliadou, C., Baou, K., Stefanadi, E. and Stefanadis, C., 2009. Divergent effects of laughter and mental stress on arterial stiffness and central hemodynamics. *Psychosomatic medicine*, *71*(4), pp.446-453.

Vrticka, P., Neely, M., Walter Shelly, E., Black, J.M. and Reiss, A.L., 2013. Sex differences during humor appreciation in child-sibling pairs. *Social neuroscience*, *8*(4), pp.291-304.

Waddington, C.H., 2017. *The nature of life*. (Digital edition), London, Routledge.

Wadsworth, B.J., 1996. *Piaget's theory of cognitive and affective development: Foundations of constructivism*. Loco, Longman Publishing.

Walker, N., 1991. Toward Solidarity: Women's Humor and Group Identity. In *Women's comic visions*, ed. Sochen, J.. Detroit, Wayne State Univ Press, pp.57-81.

Waller, B.M. and Dunbar, R.I., 2005. Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (Pan troglodytes). *Ethology*, *111*(2), pp.129-142.

Wallin, N.L., Merker, B. and Brown, S. eds., 2001. *The origins of music*. Cambridge, Ma., MIT Press.

Walpole, H., 1842. *The Letters of Horace Walpole: Earl of Orford: Including Numerous Letters Now First Published from the Original Manuscripts (Vol. 1).* London, Lea and Blanchard.

Walsh, G.L., 1979. Mutilated hands or signal stencils? A consideration of irregular hand stencils from central Queensland. *Australian Archaeology*, (9), pp.33-41.

Wan, C. and Chiu, C.Y., 2009. *An intersubjective consensus approach to culture: The role of intersubjective norms versus cultural self in cultural processes*. New York, Psychology Press.

Wang, E., Ding, Y.C., Flodman, P., Kidd, J.R., Kidd, K.K., Grady, D.L., Ryder, O.A., Spence, M.A., Swanson, J.M. and Moyzis, R.K., 2004. The genetic architecture of selection at the human dopamine receptor D4 (DRD4) gene locus. *The American Journal of Human Genetics*, *74*(5), pp.931-944.

Wang, W.B. and Lin, B., 2003. English Verbal Humour: A Cognitive Pragmatic Inquiry [J]. *Journal of Foreign Languages*, *4*, p.004.

Wang, Y., 2002. On cognitive informatics. In *Cognitive Informatics, 2002. Proceedings. First IEEE International Conference on* IEEE, pp.34-42.

Wardenaar, L.A., 1975. Humor in the Colonial Promotional Tract: Topics and Techniques. *Early American Literature*, *9*(3), pp.286-300.

Warren, J.E., Sauter, D.A., Eisner, F., Wiland, J., Dresner, M.A., Wise, R.J., Rosen, S. and Scott, S.K., 2006. Positive emotions preferentially engage an auditory–motor "mirror" system. *Journal of Neuroscience*, *26*(50), pp.13067-13075.

Watson, J.M., Mcdermott, K.B. and Balota, D.A., 2004. Attempting to avoid false memories in the Deese/Roediger—McDermott paradigm: Assessing the combined influence of practice and warnings in young and old adults. *Memory & Cognition*, *32*(1), pp.135-141.

Watson, K.K., Matthews, B.J. and Allman, J.M., 2006. Brain activation during sight gags and language-dependent humor. *Cerebral Cortex*, *17*(2), pp.314-324.

Wattendorf, E., Westermann, B., Fiedler, K., Kaza, E., Lotze, M. and Celio, M.R., 2012. Exploration of the neural correlates of ticklish laughter by functional magnetic resonance imaging. *Cerebral Cortex*, *23*(6), pp.1280-1289.

Watts, I., 2002. Ochre in the Middle Stone Age of southern Africa: Ritualised display or hide preservative?. *The South African Archaeological Bulletin*, pp.1-14.

Weaver, J. and Zillmann, D., 1994. Effect of humor and tragedy on discomfort tolerance. *Perceptual and motor skills*, *78*(2), pp.632-634.

Weinstein, D., Launay, J., Pearce, E., Dunbar, R.I. and Stewart, L., 2016. Singing and social bonding: Changes in connectivity and pain threshold as a function of group size. *Evolution and Human Behavior*, *37*(2), pp.152-158.

Weisenberg, M., Tepper, I. and Schwarzwald, J., 1995. Humor as a cognitive technique for increasing pain tolerance. *PAIN®*, *63*(2), pp.207-212.

Weisfeld, G.E., 1993. The adaptive value of humor and laughter. *Ethology and Sociobiology*, *14*(2), pp.141-169.

Wennerstrom, A., 2001. *The music of everyday speech: Prosody and discourse analysis*. Oxford, Oxford University Press.

West-Eberhard, M.J., 1979. Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society*, *123*(4), pp.222-234.

Wetzel, N., Widmann, A. and Schröger, E., 2009. The cognitive control of distraction by novelty in children aged 7–8 and adults. *Psychophysiology, 46(3),* pp.607-616.

White, R., 1992. Beyond art: toward an understanding of the origins of material representation in Europe. *Annual Review of Anthropology, 21(1)*, pp.537-564.

White, R., 2003. *Prehistoric art: the symbolic journey of humankind*. New York, Harry N. Abrams.

Whiten, A. and Byrne, R.W., 1988. Tactical deception in primates. Behavioral and brain sciences, 11(2), pp.233-244.

Whiten, A., Custance, D.M., Gomez, J.C., Teixidor, P. and Bard, K.A., 1996. Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of comparative psychology*, *110*(1), p.3.

Whiten, A., Horner, V. and Marshall-Pescini, S., 2003. Cultural panthropology. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(2), pp.92-105.

Whittlesea, B.W., 1997. Production, evaluation, and preservation of experiences: Constructive processing in remembering and performance tasks. In D. L. Medin (Ed.), *The psychology of learning and motivation: Advances in research and theory,* Vol. 37. San Diego, Academic Press, pp. 211-264.

Wilber, K., 1997. An integral theory of consciousness. *Journal of consciousness studies*, 4(1), pp.71-92.

Wild, B., Rodden, F.A., Grodd, W. and Ruch, W., 2003. Neural correlates of laughter and humour. *Brain*, *126*(10), pp.2121-2138.

Williams, J.H., Whiten, A., Suddendorf, T. and Perrett, D.I., 2001. Imitation, mirror neurons and autism. *Neuroscience & Biobehavioral Reviews*, *25*(4), pp.287-295.

Williams, R., 2009. 'Having a laugh': masculinities, health and humour. *Nursing inquiry*, *16*(1), pp.74-81.

Willmann, J.M., 1940. An analysis of humor and laughter. *The American Journal of Psychology*, *53*(1), pp.70-85.

Wilner, O.L., 1930. Contrast and Repetition as Devices in the Technique of Character Portrayal in Roman Comedy. *Classical Philology*, *25*(1), pp.56-71.

Wilson, M., 2002. Six views of embodied cognition. *Psychonomic bulletin & review*, *9*(4), pp.625-636.

Wilson-Mendenhall, C.D., Simmons, W.K., Martin, A. and Barsalou, L.W., 2013. Contextual processing of abstract concepts reveals neural representations of nonlinguistic semantic content. *Journal of cognitive neuroscience*, *25*(6), pp.920-935.

Winner, E. and Leekam, S., 1991. Distinguishing irony from deception: Understanding the speaker's second-order intention. *British journal of developmental psychology*, *9*(2), pp.257-270.

Wolff P., 1959. Observations on newborn infants. *Psychosomatic Medicine*; 21, pp.110–118.

Wolff, P., 1963. Observations on the early development of smiling. *Determinants of infant behavior*, *2*, pp.113-138.

Woods, P., 1983. Coping at school through humour. *British Journal of Sociology of Education*, *4*(2), pp.111-124.

Wooten, P., 1996. Humor: an antidote for stress. *Holistic nursing practice*, *10*(2), pp.49-56.

Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N., Brace, C.L., Bunn, H.T., Roura, E.C., Hawkes, K., O'Connell, J.F. and Blurton Jones, N.G., 1999. The raw and the stolen: cooking and the ecology of human origins. *Current anthropology*, *40*(5), pp.567-594.

Wu, W.H., Meijer, O.G., Uegaki, K., Mens, J.M.A., Van Dieen, J.H., Wuisman, P.I.J.M. and Östgaard, H.C., 2004. Pregnancy-related pelvic girdle pain (PPP), I: Terminology, clinical presentation, and prevalence. *European Spine Journal*, *13*(7), pp.575-589.

Yanagihara S*,* Hessler N.A*.,* 2006. Modulation of singing-related activity in the songbird ventral tegmental area by social context*. Eur J Neurosci 24,* pp.*3619–3627*.

Yerkes, R.M. and Yerkes, A.W., 1932. The great apes. A study of anthropoid life. *Revue Philosophique de la France Et de l'Etranger* 114, pp.464-466.

Yip, J.A. and Martin, R.A., 2006. Sense of humor, emotional intelligence, and social competence. *Journal of Research in Personality*, *40*(6), pp.1202-1208.

Yopp, H.K., 1995. Read-aloud books for developing phonemic awareness: An annotated bibliography. *The Reading Teacher*, *48*(6), pp.538-542.

Yovetich, N.A., Dale, J.A. and Hudak, M.A., 1990. Benefits of humor in reduction of threat-induced anxiety. *Psychological Reports*, *66*(1), pp.51-58.

Yus, F., 2003. Humor and the search for relevance. *Journal of pragmatics*, *35*(9), pp.1295-1331.

Zahavi, A., 1975. Mate selection—a selection for a handicap. *Journal of theoretical Biology*, *53*(1), pp.205-214.

Zalla, T. and Sperduti, M., 2013. The amygdala and the relevance detection theory of autism: an evolutionary perspective. *Frontiers in human neuroscience*, *7*, p.894.

Ziegler, J.B., 1998. Use of humour in medical teaching. *Medical Teacher*, *20*(4), pp.341-348.

Zion, I.B., Tessler, R., Cohen, L., Lerer, E., Raz, Y., Bachner-Melman, R., Gritsenko, I., Nemanov, L., Zohar, A.H., Belmaker, R.H. and Benjamin, J., 2006. Polymorphisms in the dopamine D4 receptor gene (DRD4) contribute to individual differences in human sexual behavior: desire, arousal and sexual function. *Molecular psychiatry*, *11*(8), p.782.

Ziv, A., 1988. Humor's role in married life. *Humor-International Journal of Humor Research*, *1*(3), pp.223-230.

Ziv, A., 1988. Teaching and learning with humor: Experiment and replication. *The Journal of Experimental Education*, *57*(1), pp.4-15.

Zuberbühler, K., 2000. Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*(1444), pp.713-718.

Zuckerman, M., 1984. Sensation seeking: A comparative approach to a human trait. *Behavioral and Brain Sciences, 7*, 413-471.

Zupancic, A., 2008. *The odd one in: On comedy.* Cambridge, Ma, MIT Press.