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6	Synchrony as an adaptive mechanism for large-scale human social bonding
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20 Abstract

Humans have developed a number of specific mechanisms that allow us to maintain much larger social networks than would be expected given our brain size. For our primate cousins, social bonding is primarily supported using grooming, and the bonding effect this produces is primarily mechanistically underpinned by the release of endorphins (although other neurohormones are also likely to be involved). Given large group sizes and time budgeting constraints, grooming is not viable as the primary social bonding mechanism in humans. Instead, during our evolutionary history, we developed other behaviours that helped us to feel connected to our social communities. Here we propose that synchrony might act as direct means to encourage group cohesion by causing the release of neurohormones that influence social bonding. By acting on ancient neurochemical bonding mechanisms, synchrony can act as a primal and direct social bonding agent, and this might explain its recurrence throughout diverse human cultures and contexts (e.g. dance, prayer, marching, music-making). Recent evidence supports the theory that endorphins are released during synchronised human activities, including sport, but particularly during musical interaction. Thus synchrony-based activities are likely to have developed due to the fact that they allow the release of these hormones in large-scale human communities, providing an alternative to social bonding mechanisms such as grooming.

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Synchrony as an adaptive mechanism for large-scale human social bonding

Humans, like most anthropoid primates, live in bonded social groups (Dunbar & Shultz 2010) which allow members to directly influence fitness by buffering individuals against the stresses of social life (Wittig et al. 2008), enhancing infant survival (Flinn & England 1995; Silk et al. 2003; Silk 2007; Oesch & Dunbar 2015) and mounting coordinated defence against predators or raiders (Dunbar et al. 2014). During the process of human evolution, maintaining relationships with members of our social networks has become increasingly important to our health and wellbeing (Berkman 1984; Holt-Lunstad et al. 2010), so while our closest primate relatives have social network sizes that are directly predicted by brain size (Dunbar 1992; Kudo & Dunbar 2001), we have developed the ability to form larger networks than should be cognitively feasible. The predicted upper limit to the number of possible human social relationships (150; Dunbar 1992) is applicable to a wide variety of interpersonal situations, including hunter-gatherer clans (Dunbar 1993), Christmas card networks (Hill & Dunbar 2003), and active Facebook relationships (Arnaboldi et al. 2013; Dunbar et al. 2015; Dunbar 2016), yet we can also experience a sense of connection with larger groups.

Primates bond their groups through social grooming, and the linear relationship between group size and the time devoted to grooming across species (Dunbar 1991; Lehmann et al. 2007; Dunbar & Lehmann 2013) appears to set an upper limit on the size of group that can be so bonded at around 50 individuals. Time invested in a relationship is important in order to gain benefits from social interaction, since relationship quality appears to reflect the time invested in it (Sutcliffe et al. 2012). However, since the number of hours in a day is limited (even if extended using fire: c.f. Dunbar 2014a), bonding larger groups than those typical of non-human primates makes it necessary to develop behaviors that use time more efficiently so as to allow bonding between multiple individuals simultaneously (Dunbar 2012). Humans might first have had to find solutions to these time constraints, then during

the development of increasingly large social networks repeatedly adopted new cognitive, technological and sociological mechanisms to maintain cohesion. Here we argue that human social behaviours that involve synchronised movements (e.g. sport, music, ritual) can be understood as technologies developed to exploit existing neurobiological and psychological mechanisms which are important in the maintenance of social bonds. Synchronisation might initially have helped save time when socially bonding but recent evidence suggests, in the case of singing, it can encourage social bonding in groups larger than 150 people (Weinstein et al. 2015). Although unlikely to have increased cognitive constraints on the number of genuine social ties that can exist this might demonstrate humans experiencing connection to a larger social group to which others are associated, and thus a sense of shared communities with those others. Music and dance are particularly well investigated examples of social synchronisation, and here we focus on these examples, although further research into activities such as sport and exercise is also warranted (c.f. Launay 2015a).

1. The neurobiology of social bonding

Over the past fifteen years, there has been a surge in interest in the neurobiological underpinnings of social bonding, across mammal species including humans (Young & Wang 2004; Lim & Young 2006; e.g. Insel 2010). A large part of this interest originated from research in species of monogamous and non-monogamous voles, which suggested that larger numbers of receptors for the neuropeptide oxytocin are associated with monogamous behaviour (Insel & Shapiro 1992), but that this monogamous behaviour can be blocked with a selective oxytocin antagonist (Young et al. 2001). Administration of oxytocin has for a long time been known to play a role in birth, lactation, and maternal behaviour (Pedersen & Prange 1979), and given this relationship with monogamy oxytocin became a good candidate

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as a 'social' neuropeptide. Early experimental studies in humans demonstrated, for example, a relationship between oxytocin and increased trust (Kosfeld et al. 2005; Zak et al. 2005), eye contact (Guastella et al. 2008), face memory (Savaskan et al. 2008), generosity (Zak et al. 2007), empathy and the ability to infer the mental state of others (Domes et al. 2007). More recently, the administration of oxytocin in humans has been shown to have positive effects towards both one's own in-group (e.g. De Dreu et al. 2011) and out-groups (Shamay-Tsoory et al. 2013), with individual differences predicting some of this variability in behaviour (Ma et al. 2015) This suggests that the effects of oxytocin generalise beyond dyadic bonding, although more research is required to fully clarify these effects (Nave et al. 2015).

Although oxytocin plays a role in human social bonding, there is reason to doubt that it is the only important social neurohormone in humans. Humans have a uniquely high propensity to form social bonds with unrelated others (e.g. Dunbar & Shultz 2010), and it is likely that this tendency is supported by an array of cognitive and neurobiological mechanisms, almost certainly co-opted from neural systems that existed before we developed such a large dependence on our social networks. Evidence indeed demonstrates that there are multiple neurohormonal cascades involved in social bonding, which include not just oxytocin and vasopressin (e.g. Carter 1998) but also neurotransmitters such as dopamine and serotonin (e.g. Depue & Morrone-Strupinsky 2005), endocannabinoids (e.g. Trezza & Vanderschuren 2008) and the Endogeonous Opioid System (EOS; Curley & Keverne 2005; Dunbar 2010; Machin & Dunbar 2011). While all of these pathways are likely to play some part in social bonding that occurs between unrelated humans, here we concentrate on the role of endorphins because there is a substantial body of evidence suggesting that these play an especially important role in social bonding with unrelated conspecifics in non-human primates (e.g. Meller et al. 1980), and that the system may be activated by physiological arousal (Howlett et al. 1984; Harbach et al. 2000).

The EOS is central in opioid-mediated reward (Koob 1992; Olmstead & Franklin 1997; Comings et al. 1999), social motivation (Chelnokova et al. 2014), and pleasure and pain perception (Janal et al. 1984; Leknes & Tracey 2008), and is associated with feelings of euphoria (Boecker et al. 2008). The capacity for experiencing (positively reinforcing) endorphin-related euphoria in a social setting is likely to encourage further interaction with individuals who are present, making this neuropeptide a good candidate (from an evolutionary perspective) for promoting social bonding. In addition, its opiate-like properties of inducing relaxation and calmness may be instrumental in creating a sense of trust. In an environment where the formation of closer social bonds is advantageous those behaviours that encourage the release of endorphins in social situations are likely to be positively selected for.

Evidence from non-human primates provides strong support that social bonding activities are associated with activity of the EOS. An early finding demonstrated that male talapoin monkeys administered with an endorphin receptor antagonist did not exhibit increased sexual behaviour (as occurs in rats) but instead showed increased rates of dyadic grooming (Meller et al. 1980). This result was replicated by Fabre-Nys (1982), and supported in the same species through direct measurement of central nervous system levels of betaendorphins, which were found to be higher following grooming (Keverne et al. 1989; Martel et al. 1995). Given that grooming is thought to be used by non-human primates to reinforce social bonds and maintain peaceful relations and social cohesion, these results suggest that in primate evolutionary history the opioid system was co-opted to mechanistically support our need for enhanced social bonds (e.g. Curley & Keverne, 2005; Lehmann et al. 2007).

In humans, there is less direct evidence about the relationship between social behaviour and the endogenous opioid system, but the Brain Opioid Theory of Social Attachment (BOTSA) argues that there are notable similarities in the behaviour and emotions

of people addicted to exogenous opiates and people in intense relationships (Panksepp 1999; Insel 2003). Early stages of opiate addiction and intense relationships both involve euphoria, with feelings of pleasure and gratification leading to a desire to continuously seek out the stimulus (Machin & Dunbar 2011; Eisenberger 2012). Furthermore there is some experimental evidence to suggest that interfering with the activity of the EOS in humans can affect the way that positive social stimuli are perceived (Chelnokova et al. 2014), and that areas of the brain with high concentrations of opioid receptors are responsive to social rejection and acceptance (Hsu et al. 2013; Eisenberger 2015). In summary, while evidence is primarily correlational, BOTSA illustrates that for humans both social attachment and the administration of exogenous opiates have similar neurophysiological effects (Nelson & Panksepp 1998; Nummenmaa et al. 2016).

In addition to their potential role in social behaviour opioids are known to be released in response to low levels of muscular and psychological stress (Howlett et al. 1984), for example during exercise (Harbach et al. 2000), with evidence suggesting that the euphoric state that follows exercise (termed 'runner's high') is due to endogenous opioids (Boecker et al. 2008). Further to the effect on mood, opioids have a very strong analgesic effect (Van Ree et al. 2000), being some 30 times more potent than morphine on a weight-for-weight basis (Loh et al.1976), and much evidence suggests that endorphins are central in the pain management system (Levine et al. 1979; Basbaum & Fields 1984; Janal et al. 1984; D'Amato & Pavone 1993; Benedetti 1996; Zubieta et al. 2001; Fields 2007; Bodnar 2008; Dishman & O'Connor 2009; Mueller et al. 2010). The release of endorphins during strenuous exercise has both pain relieving and euphoric effects, increasing the positive reinforcement for an individual.

Given that direct measures of endogenous opioids are costly and invasive in humans (Dearman & Francis 1983), pain threshold is commonly used as a proxy measure of

endorphin release, and this has been operationalised using the length of time holding a hand in ice water or a frozen vacuum sleeve on the arm (Depue & Morrone-Strupinsky 2005; Dunbar et al. 2012a, b), a ski exercise (maintaining a squat position with legs at right angles: Dunbar et al. 2012a), an electrocutaneous simulator (Jamner & Leigh 1999), pressure produced using a blood pressure cuff (Cogan et al. 1987; Cohen & Ejsmond-Frey 2010; Dunbar et al. 2012a, b), and the amount of pain medication requested by patients (Zillmann et al. 1993). Given the evidence that endorphins act as analgesics, previous studies have used changes in pain thresholds as an indicator of central endorphin release following a relevant activity (e.g. engaging in sports).

According to the pain threshold assay, various exertive human social bonding activities have an impact on endorphin release. A series of five experiments demonstrated that pain thresholds are significantly increased as a consequence of laughter whilst watching humorous videos (or live stand-up comedy) over non-humorous videos (or live drama), but that a social context was required in order to evince this effect (Dunbar et al. 2012a). That it is specifically endorphins that are involved in this has since been confirmed using positron emission tomography (PET: Nummenmaa et al 2016). Studies in which people were asked to exercise on rowing machines have demonstrated that exertive activity in the presence of other people leads to a greater increase in pain thresholds than when alone, and that this can occur in either the presence of known others, or with strangers (Cohen & Ejsmond-Frey 2010; Sullivan & Rickers 2013).

This area of research has begun to demonstrate that synchronised exertive activities can lead to a greater increase in pain thresholds than unsynchronised activities (Sullivan et al. 2014; Tarr et al. 2016). Importantly, the effects of synchronisation and exertion appear to be additive, with each contributing towards an increase in pain thresholds independently (Tarr et al. 2015), suggesting that activities which include both of synchrony and exertion might be

considered 'ideal' for the release of endorphins. In the following section we review this evidence and will later return to our reasons to associate endorphin release and synchronisation, using musical activities as an example of human activity that engages this system.

2. Synchronisation and social bonding

Synchronisation has, in the past few years, come under experimental investigation as a potential means by which humans can become more socially bonded with one another (Hove & Risen 2009; Wiltermuth & Heath 2009; Valdesolo & Desteno 2011; Launay et al. 2013). It has long been argued that synchronisation and social bonding are related, based on, for example, the known bonding effects of activities such as marching (McNeill 1995) and evidence which demonstrates there is a reciprocal effect between mimicry and social bonding (Chartrand et al. 2005). 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.

People have a tendency to spontaneously synchronise their movements with those of other people, and this can happen unintentionally, and even when instructed not to do so (Issartel et al. 2007; Oullier et al. 2008; van Ulzen et al. 2008). Prosocial people will demonstrate more spontaneous synchronisation than people with pro-self tendencies (Lumsden et al. 2012), and priming to believe that someone is more socially desirable can encourage synchronisation between strangers (Miles et al. 2010, 2011), suggesting that interpersonal synchronisation is a social and facilitative behaviour, rather than an automatic motor process. People also report perceived synchrony to be an indicator of social closeness between people for both basic sounds (Miles et al. 2009; Lakens & Stel 2011) and musical

stimuli (Hagen & Bryant 2003), suggesting that the tendency to associate synchronisation with social behaviour is well engrained.

Importantly, there is recent evidence to show that that synchronisation between strangers can have effects on subsequent measures of social bonding (Hove & Risen 2009; Wiltermuth & Heath 2009; Valdesolo & Desteno 2011; Launay et al. 2013). This has been demonstrated in a number of experimental studies in which participants tapping synchronously with an experimenter (Hove & Risen 2009; Valdesolo & Desteno 2011), walk in time with other people (Wiltermuth & Heath 2009; Wiltermuth 2012) or dance together (Reddish et al. 2013), even when people have no visual access to one another but are synchronising with the sounds of another person (Kokal et al. 2011; Launay et al. 2014). These effects are also present throughout development (Kirschner & Tomasello 2010; Cirelli et al. 2014a, b; Tunçgenç et al. 2015), suggesting that, if they are learned, this happens very early in life.

In general, the social bonding effects of synchronisation have been attributed to selfother blurring that might occur any time we match our movements exactly to the movements
of another person (e.g. Decety & Sommerville 2003). Perception of the movements of
another person is known to activate regions of the brain involved in making a similar
movement ourselves (e.g. Gallese et al. 1996; Rizzolatti & Craighero 2004), which means
that moving at the same time as another person leads to co-activation of similar neural
networks for perception and action. The Rubber Hand Illusion has demonstrated that it is
possible to perceive a sense of ownership over a rubber hand when feeling a stroking motion
synchronously with observing the hand being stroked (Botvinick & Cohen 1998), implying
that blurring of self and other is possible even in the case of cross-modal perceptual inputs.
However, this self-other matching process is likely to account for only some of the social
bonding effects of real synchronous human activities, such as dance, where there are likely to

be many people involved, movements that are not exactly matched between co-actors, and associations with an external source, such as music.

From an evolutionary perspective an important potential reason for synchronised activities to be socially bonding might be that they play a role in lekking (e.g. Ryder et al. 2011). When engaging in chorused activities, all-male bands of several species appear to be able to attract females to their group due to the quality of the display (e.g. Merker 2000). It would therefore seem logical that group members who are particularly capable or competent should be sought out so as to enhance the quality of chorusing bouts. This might form part of the origins of synchronised activities (Merker et al. 2009), but the lack of clear sexual dimorphism in human abilities for synchronisation suggest that this is unlikely to be the only purpose that these activities serve (Bowling et al. 2013). Synchronised activities could have developed as a method for attracting mates, but then also served to aid evaluation of same-sex companions, and a demonstration of a group's prowess or power. The knowledge gleaned of same-sex companions could prove to be useful in determining group membership, making it beneficial to co-opt these activities for social bonding purposes. Hitherto, it is only possible to speculate on the extent to which this capacity has been consciously used to promote and assess cohesion throughout history, but one recent study has shown that people moving in synchrony are perceived as more formidable (e.g. Fessler & Holbrook 2016).

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3. Music, social bonding and the Endogenous Opioid System

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So far we have reviewed evidence which demonstrates that the endogenous opioid system is involved in primate social bonding, and that the act of synchronising with other people can lead to social bonding. Here we connect these two lines of research, and suggest that synchronised musical activities are particularly conducive to the release of endorphins, by

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virtue of encouraging exertive movement in the presence of other people, and as a consequence of engaging regions of the brain involved in movement and social cognition.

Based on the recent evidence associating exertive activities and endorphin release (e.g. Cohen & Eismond-Frey 2010; Sullivan & Rickers 2013; Tarr et al. 2015), a small number of studies have started to investigate the effect of active engagement in musical activities and the EOS. For example, sufficiently vigorous singing, dancing and drumming trigger a significantly larger increase in both pain threshold and positive affect compared to listening to music and engaging in low energy musical activities, suggesting that physical activity is important in the relationship between music, endorphins and social bonding (Dunbar et al. 2012b; Tarr et al. 2015). Another recent set of studies connected exercise machines to musical output software so that individuals influenced a musical soundscape though the exertive movements they made: when movement during group exercise resulted in musical feedback, participants perceived their own exertion to be lower, reported enhanced mood, and felt a greater desire to exert themselves further in comparison with when they were exercising whilst listening (passively) to music that they had no control over (Fritz et al. 2013a, b). As such, musical agency (i.e. perception of a relationship between purposeful movement and sounds that are being produced) is likely to be associated with greater endorphin release, again suggesting that there is an important relationship between exertive movements, music and the EOS.

However, the release of endorphins as a consequence of engaging with music is not limited to situations involving exertion. There is a considerable amount of evidence to suggest that listening to music can reduce perception of pain (Koch et al. 1998; Allen et al. 2001; Good et al. 2001; Lepage et al. 2001; Nilsson et al. 2001, 2003; Nilsson 2008) and therefore diminish the need for opioid agonists following operative care (Cepeda & Carr 2006; Bernatzky et al. 2011). This effect is largely attributed to the activity of the EOS,

suggesting that listening to music alone can have similar effects on endorphins to those experienced when actively engaging in musical activities.

More direct evidence using positron emission tomography has demonstrated that the EOS is engaged during passive listening to music (Blood & Zatorre 2001; Stefano et al. 2004). Functional Magnetic Resonance Imaging has provided evidence that areas of the brain with large numbers of opioid receptors that are involved in positive reinforcement (such as the nucleus accumbens) are active during passive listening to music (Brown et al. 2004; Menon & Levitin 2005; Koelsch 2014). The argument for a role of the EOS in musical experiences is strengthened by evidence associating 'thrills' and a sense of elation experienced whilst listening to music with endorphins (Goldstein 1980; Chiu & Kumar 2003). As well as calming music buffering stressful life events (see McKinney et al. 1997 for a review), it has been argued that listening to techno music significantly changes emotional states (and increases beta-endorphin levels) due to its strong rhythmic beat and engagement of motor regions of the brain (Gerra et al. 1998).

This suggests that exertion is not necessarily required for music to engage the EOS, and that the analgesic effects of listening to music are not simply attributable to its relaxing properties. It is important to return to the ubiquitous human aptitude for entrainment to rhythmic beats (Clayton et al. 2005; Brown & Jordania 2011), particularly those embedded in music (e.g. Demos et al. 2012) and, in addition, the detection of human agency, which is inextricably linked with the detection of rhythm and the desire to engage with that rhythm (Launay 2015b). Being told that music is created by a person rather than a computer means that listening to that music engages regions of the brain involved in social cognition, as well as motor regions of the brain (Steinbeis & Koelsch 2009). People synchronise differently when they believe they are interacting with a human compared with a computer (Konvalinka et al. 2010), and children's drumming performance is improved when they believe they are

interacting with another person (Kirschner & Tomasello 2009). Importantly this might mean that even in the absence of another person musical and rhythmic sounds are detected as having some sense of agency, leading to some subjective social experience (Launay 2015b). Given that synchronisation and social bonding are thought to be linked via self-other coupling it is feasible that musical sounds, by virtue of the identification of agency, and musical rhythm (Zatorre et al. 2007; which engages motor regions of the brain: Chen et al. 2008) leads to some imagined protosocial experience, and this has some influence on the EOS. This is somewhat speculative and needs much further investigation, but does suggest an evolutionary time course from making movements together to the pleasure and enjoyment we currently derive from listening to music alone.

4. A proposed evolutionary time course from endorphins to music via synchronisation

At some point in primate history it became important to engage in social activities with non-related conspecifics. Endorphins were co-opted from existing neural systems for pain management, as it was relatively easy to encourage their release through mildly stimulating interpersonal contact (Curley & Keverne 2005). However, as hominids started to rely on increasingly large social groups there was a need to 'groom at a distance', requiring new behaviours that allowed the release of endorphins without physical touch (Dunbar 2012).

Estimates of the time budgets for the main hominin taxa (based on calculations given in Dunbar 2014b) suggest that without finding mechanisms for drastically reducing the costs of social bonding as well as foraging, hominin time budgets would have been unsustainable had they needed to live in larger groups than those characteristic of the most social monkeys and apes. In the case of anatomically modern humans, the gross time budget would have exceeded available active day time (defined by tropical daylight) by more than 50%. Social

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grooming is extremely expensive time-wise (Dunbar 1991; Lehmann et al. 2007) because it is a strictly one-on-one activity. Hence, one effective way of reducing the time costs of social bonding is to increase the size of the 'grooming' group so that more individuals can be 'groomed' simultaneously.

Synchronisation and physical exertion in social settings allow both the co-ordination of groups of people, and the release of endorphins though exertive motor activity, effectively taking on the role previously filled by grooming. As well as solving problems of time constraints these activities could make groups larger than 150 feel socially connected very quickly (Pearce et al. 2015; Weinstein et al. 2015), although this connection is likely to be felt towards the group as a whole rather than experienced as individual social relationships (Pearce et al. in press). Forms of synchronised movement could have progressively evolved and become positively reinforcing in their own right. When perceiving the music of the people from our own social group, and correctly predicting the repetitive rhythms involved we perform some mental synchronisation with those human driven sounds. While exertion is no longer a necessity for experiencing a social high during musical activities, it inevitably boosts the release of endorphins, meaning that active engagement in musical activities is optimal for social bonding, although passive listening can be sufficient to lead to the release of endorphins with some consequent analgesic effects. Importantly, as we noted above, both synchronisation and exertive engagement have independent effects on activation of the EOS and social closeness experienced by people engaging in musical activities together.

While this series of events cannot be verified, it should nonetheless be possible to bring further evidence to bear on the question. More thorough testing of the relationship between synchronisation, exertion, endorphins and social bonding might help to elucidate potential causal pathways by which synchronous activities such as dance influence social bonds more generally. In addition, our current understanding of the degree to which musical

sounds are perceived as agent driven and the underlying neural mechanisms that relate to these differences in perception are relatively poor. By bringing these lines of evidence together, it should be possible to determine the importance that synchronisation plays in our social experience of musical activities, both passive and involving active performance.

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References 380 Allen, K., Golden, L.H., Izzo, J.L., Ching, M.I., Forrest, A., Niles, C.R., Niswander, P.R. and 381 Barlow, J.C. 2001: Normalization of hypertensive responses during ambulatory surgical 382 stress by perioperative music. Psychosomatic Medicine 63, 487–492. 383 Arnaboldi, V., Conti, M., Passarella, A. and Dunbar, R.I.M. 2013: Dynamics of personal 384 social relationships in online social networks: a study on Twitter. Proceedings of the 1st 385 ACM Conference on Online Social Networks, 15–26. 386 Basbaum, A.I. and Fields, H.L. 1984: Endogenous Pain Control Systems: Brainstem Spinal 387 Pathways and Endorphin Circuitry. Annual Review of Neuroscience 7, 309–338. 388 Benedetti, F. 1996: The opposite effects of the opiate antagonist naloxone and the 389 cholecystokinin antagonist proglumide on placebo analgesia. Pain 64, 535–543. 390 Berkman, L. 1984: Assessing the physical health effects of social networks and social 391 support. Annual Review of Public Health 5, 413–432. 392 393 Bernatzky, G., Presch, M., Anderson, M. and Panksepp, J. 2011: Emotional foundations of music as a non-pharmacological pain management tool in modern medicine. 394 Neuroscience and Biobehavioral Reviews 35, 1989–1999. 395 Blood, A.J. and Zatorre, R.J. 2001: Intensely pleasurable responses to music correlate with 396 activity in brain regions implicated in reward and emotion. Proceedings of the National 397 Academy of Sciences of the United States of America 98, 11818–11823. 398 Bodnar, R.J. 2008: Endogenous opiates and behavior: 2007. Peptides 29, 2292-2375. 399 400 Boecker, H., Sprenger, T. and Spilker, M. 2008: The runner's high: opioidergic mechanisms in the human brain. Cerebral Cortex 18, 2523-2531. 401 Botvinick, M. and Cohen, J. 1998: Rubber hands 'feel' touch that eyes see. Nature 391, 756. 402 Bowling, D.L., Herbst, C.T. and Fitch, W.T. 2013: Social origins of rhythm? Synchrony and 403 temporal regularity in human vocalization. PloS one, e80402. 404 405 Brown, S. and Jordania, J. 2011: Universals in the world's musics. Psychology of Music 41, 229–248. 406 Brown, S., Martinez, M.J. and Parsons, L.M. 2004: Passive music listening spontaneously 407 engages limbic and paralimbic systems. Neuroreport 15, 2033–2037. 408 Carter, C.S. 1998: Neuroendocrine perspectives on social attachment and love. 409 Psychoneuroendocrinology 23, 779–818. 410 Cepeda, M. and Carr, D. 2006: Music for pain relief. The Cochrane Library 2. 411

- Chartrand, T.L., Maddux, W.W. and Lakin, J.L. 2005: Beyond the perception-behavior link:
- the ubiquitous utility and motivational moderators of nonconscious mimicry. In Hassin,
- 414 R. R., Uleman, J. S., Bargh, J. A. (eds.), The New Unconscious, 334–361. Oxford
- 415 University Press, New York.
- Chelnokova, O., Laeng, B., Eikemo, M., Riegels, J., Løseth, G., Maurud, H., Willoch, F. and
- Leknes, S. 2014: Rewards of beauty: the opioid system mediates social motivation in
- humans. Molecular Psychiatry **19**, 746–747.
- Chen, J.L., Penhune, V.B. and Zatorre, R.J. 2008: Listening to musical rhythms recruits
- motor regions of the brain. Cerebral Cortex 18, 2844–2854.
- 421 Chiu, P. and Kumar, A. 2003: Music therapy: Loud noise or soothing notes. International
- 422 Pediatrics **18**, 204–208.
- 423 Cirelli, L.K., Einarson, K.M. and Trainor, L.J. 2014a: Interpersonal synchrony increases
- prosocial behavior in infants. Developmental Science 17, 1003–1011
- 425 Cirelli, L.K., Wan, S. and Trainor, L. 2014b: Fourteen-month-old infants use interpersonal
- synchrony as a cue to direct helpfulness. Philosophical Transactions of the Royal
- Society B: Biological Science **369**, 20130.
- Clayton, M., Sager, R. and Will, U. 2005: In time with the music: the concept of entrainment
- and its significance for ethnomusicology. European Journal of Social Psychology 11, 3–
- 430 142.
- Cogan, R., Cogan, D., Waltz, W. and McCue, M. 1987: Effects of laughter and relaxation on
- discomfort thresholds. Journal of Behavioral Medicine **10**, 139–144.
- Cohen, E.E.A. and Ejsmond-Frey, R. 2010: Rowers' high: behavioural synchrony is
- correlated with elevated pain thresholds. Biology Letters **6**, 106–108.
- Comings, D.E., Blake, H., Dietz, G., Gade-Andavolu, R., Legro, R.S., Saucier, G., Johnson,
- P., Verde, R. and MacMurray, J.P. 1999: The proenkephalin gene (PENK) and opioid
- dependence. Neuroreport **10**, 1133–1135.
- Curley, J.P. and Keverne, E.B. 2005: Genes, brains and mammalian social bonds. Trends in
- 439 Ecology & Evolution **20**, 561–567.
- D'Amato, F.R. and Pavone, F. 1993: Endogenous opioids: a proximate reward mechanism
- for kin selection? Behavioral and neural biology **60**, 79–83.
- Dearman, J. and Francis, K.T. 1983: Plasma levels of catecholamines, cortisol, and beta-
- endorphins in male athletes after running 26.2, 6, and 2 miles. Journal of Sports
- Medicine and Physical Fitness **23**, 30–38.
- Decety, J. and Sommerville, J.A. 2003: Shared representations between self and other: a
- social cognitive neuroscience view. Trends in Cognitive Sciences 7, 527–533.

- De Dreu, C.K.W., Greer, L.L., Van Kleef, G.A., Shalvi, S. and Handgraaf, M.J.J. 2011:
- Oxytocin promotes human ethnocentrism. Proceedings of the National Academy of
- 450 Sciences **108**, 1262–1266.
- Demos, A.P., Chaffin, R., Begosh, K.T., Daniels, J.R. and Marsh, K.L. 2012: Rocking to the
- beat: Effects of music and partner's movements on spontaneous interpersonal
- 453 coordination. Journal of Experimental Psychology: General 141, 49–53.
- Depue, R.A. and Morrone-Strupinsky, J. V. 2005: A neurobehavioral model of affiliative
- bonding: implications for conceptualizing a human trait of affiliation. The Behavioral
- 456 and brain sciences **28**, 313–350.
- Dishman, R.K. and O'Connor, P.J. 2009: Lessons in exercise neurobiology: The case of
- endorphins. Mental Health and Physical Activity 2, 4–9.
- Domes, G., Heinrichs, M., Michel, A., Berger, C. and Herpertz, S.C. 2007: Oxytocin
- improves 'mind-reading' in humans. Biological Psychiatry **61**, 731–733.
- Dunbar, R.I.M. 1991: Functional significance of social grooming in primates. Folia
- 462 Primatologica **57**, 121–131.
- Dunbar, R.I.M. 1992: Neocortex size as a constraint size in primates. Journal of Human
- 464 Evolution **22**, 469–493.
- Dunbar, R.I.M. 1993: Coevolution of neocortical size, group size and language in humans.
- Behavioral and Brain Sciences **16**, 681–735.
- Dunbar, R.I.M. 2010: The social role of touch in humans and primates: behavioural function
- and neurobiological mechanisms. Neuroscience and Biobehavioral Reviews **34**, 260–
- 469 268.
- Dunbar, R.I.M. 2012: Bridging the bonding gap: the transition from primates to humans.
- 471 Philosophical Transactions of the Royal Society B: Biological Sciences **367**, 1837–1846.
- Dunbar, R.I.M. 2014a: How conversations around campfires came to be. Proceedings of the
- National Academy of Sciences USA. 111, 14013-14014.
- Dunbar, R.I.M. 2014b: Human Evolution. Pelican, London.
- Dunbar, R.I.M. 2016: Do online social media cut through the constraints that limit the size of
- offline social networks? Royal Society Open Science. doi: 10.1098/rsos.150292
- Dunbar, R.I.M., Korstjens, A.H. and Lehmann, J. 2009: Time as an ecological constraint.
- 478 Biological Reviews **84**, 413–429.
- Dunbar, R.I.M. and Shultz, S. 2010: Bondedness and sociality. Behaviour 147, 775–803.
- Dunbar, R.I.M., Baron, R., Frangou, A., Pearce, E., Van Leeuwen, E.J.C., Stow, J., Partridge,
- G., MacDonald, I., Barra, V. and van Vugt, M. 2012a: Social laughter is correlated with

- an elevated pain threshold. Proceedings of The Royal Society B. Biological Sciences **279**, 1161–1167.
- Dunbar, R.I.M., Kaskatis, K., MacDonald, I. and Barra, V. 2012b: Performance of music elevates pain threshold and positive affect: implications for the evolutionary function of music. Evolutionary Psychology **10**, 688–702.
- Dunbar, R.I.M. & Lehmann, J. 2013: Grooming and social cohesion in primates: a comment on Grueter et al. Evolution and Human Behavior **34**, 453–455.
- Dunbar, R., Lehmann, J., Korstjens, A. and Gowlett, J. 2014: The road to modern humans:
- time budgets, fission-fusion sociality, kinship and the division of labour in hominin
- 491 evolution. In Dunbar, R., Gamble, C., Gowlett, J. (eds.), Lucy to Language: The
- 492 Benchmark Papers, 333–355. Oxford University Press, Oxford.
- Dunbar, R.I.M., Arnaboldi, V., Conti, M. and Passarella, A. 2015: The structure of online social networks mirrors those in the offline world. Social Networks **43**, 39–47.
- Eisenberger, N. 2012: The pain of social disconnection: examining the shared neural underpinnings of physical and social pain. Nature Reviews Neuroscience **13**, 421–434.
- Eisenberger, N.I. 2015: Social Pain and the Brain: Controversies, Questions, and Where to Go from Here. Annual Review of Psychology **66**, 601–629.
- Fabre-Nys, C., Meller, R.E. and Keverne, E.B. 1982: Opiate antagonists stimulate affiliative behaviour in monkeys. Pharmacology, Biochemistry, and Behavior **16**, 653–659.
- Fessler, D.M. and Holbrook, C. 2016: Synchronized behavior increases assessments of the formidability and cohesion of coalitions. Evolution and Human Behavior. doi:
- 503 10.1016/j.evolhumbehav.2016.05.003
- Fields, H.L. 2007: Understanding how opioids contribute to reward and analgesia. Regional Anesthesia and Pain Medicine **32**, 242–246.
- Flinn, M. V. and England, B.G. 1995: Childhood Stress and family environment. Current Anthropology **36**, 854–866.
- Fritz, T.H., Hardikar, S., Demoucron, M., Niessen, M., Demey, M., Giot, O., Li, Y., Haynes,
- J.-D., Villringer, A. and Leman, M. 2013a: Musical agency reduces perceived exertion
- during strenuous physical performance. Proceedings of the National Academy of
- Sciences of the United States of America **110**, 17784–17789.
- Fritz, T.H., Halfpaap, J., Grahl, S., Kirkland, A. and Villringer, A. 2013b: Musical feedback during exercise machine workout enhances mood. Frontiers in Psychology 4, 921.
- Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti, G. 1996: Action recognition in the premotor cortex. Brain **119**, 593–609.
- Gerra, G., Zaimovic, A, Franchini, D., Palladino, M., Giucastro, G., Reali, N., Maestri, D.,
- Caccavari, R., Delsignore, R. and Brambilla, F. 1998: Neuroendocrine responses of

- healthy volunteers to 'techno-music': relationships with personality traits and emotional
- state. International journal of psychophysiology: official journal of the International
- Organization of Psychophysiology **28**, 99–111.
- 521 Goldstein, A. 1980: Thrills in response to music and other stimuli. Physiological Psychology
- **8**, 126–129.
- Good, M., Stanton-Hicks, M., Grass, J. A, Anderson, G.C., Lai, H.L., Roykulcharoen, V. and
- Adler, P. a. 2001: Relaxation and music to reduce postsurgical pain. Journal of
- 525 Advanced Nursing **33**, 208–215.
- Guastella, A.J., Mitchell, P.B. and Dadds, M.R. 2008: Oxytocin increases gaze to the eye
- region of human faces. Biological Psychiatry **63**, 3–5.
- Hagen, E.H. and Bryant, G. a. 2003: Music and dance as a coalition signalling system.
- 529 Human Nature **14**, 21–51.
- Harbach, H., Hell, K., Gramsch, C., Katz, N., Hempelmann, G. and Teschemacher, H. 2000:
- Beta-endorphin (1-31) in the plasma of male volunteers undergoing physical exercise.
- Psychoneuroendocrinology **25**, 551–562.
- Hill, R. and Dunbar, R.I.M. 2003: Social network size in humans. Human Nature 14, 53–72.
- Holt-Lunstad, J., Smith, T.B. and Layton, J.B. 2010: Social relationships and mortality risk: a
- meta-analytic review. PLoS medicine 7, e1000316.
- Hove, M. and Risen, J. 2009: It's all in the timing: Interpersonal synchrony increases
- affiliation. Social Cognition **27**, 949–960.
- Howlett, T., Tomlin, S. and Ngahfoong, L. 1984: Release of beta endorphin and met-
- enkephalin during exercise in normal women: response to training. British Medical
- Journal 288, 1950–1952.
- Hsu, D.T., Sanford, B.J., Meyers, K.K., Love, T.M., Hazlett, K.E., Wang, H., Ni, L., Walker,
- S.J., Mickey, B.J., Korycinski, S.T., Koeppe, R. a, Crocker, J.K., Langenecker, S. a and
- Zubieta, J.-K. 2013: Response of the μ-opioid system to social rejection and acceptance.
- Molecular Psychiatry **18**, 1211–1217.

Insel, T.R. 2003: Is social attachment an addictive disorder? Physiology & Behavior 79, 351–

- 546 357.
- Insel, T.R. 2010: The challenge of translation in social neuroscience: a review of oxytocin,
- vasopressin, and affiliative behavior. Neuron **65**, 768–779.
- Insel, T.R. and Shapiro, L.E. 1992: Oxytocin receptor distribution reflects social organization
- in monogamous and polygamous voles. Proceedings of the National Academy of
- Sciences of the United States of America **89**, 59815.
- Issartel, J., Marin, L. and Cadopi, M. 2007: Unintended interpersonal co-ordination: 'can we
- march to the beat of our own drum?'. Neuroscience Letters **411**, 174–179.

- Jamner, L.D. and Leigh, H. 1999: Repressive/defensive coping, endogenous opioids and 554 health: how a life so perfect can make you sick. Psychiatry Research 85, 17–31. 555
- Janal, M.N., Colt, E.W., Clark, W.C. and Glusman, M. 1984: Pain sensitivity, mood and 556
- plasma endocrine levels in man following long-distance running: effects of naloxone. 557
- Pain 19, 13–25. 558
- Keverne, E.B., Martensz, N.D. and Tuite, B. 1989: Beta-endorphin concentrations in 559
- cerebrospinal fluid of monkeys are influenced by grooming relationships. 560
- Psychoneuroendocrinology 14, 155–161. 561
- Kirschner, S. and Tomasello, M. 2009: Joint drumming: social context facilitates 562
- synchronization in preschool children. Journal of Experimental Child Psychology 102, 563
- 299–314. 564
- Kirschner, S. and Tomasello, M. 2010: Joint music making promotes prosocial behavior in 4-565
- year-old children. Evolution and Human Behavior 31, 354–364. 566
- Koch, M.E., Kain, Z.N., Ayoub, C. and Rosenbaum, S.H. 1998: The Sedative and Analgesic 567
- Sparing Effect of Music. Anesthesiology **89**, 300–306. 568
- Koelsch, S. 2014: Brain correlates of music-evoked emotions. Nature Reviews Neuroscience 569
- **15**, 170–180. 570
- Kokal, I., Engel, A., Kirschner, S. and Keysers, C. 2011: Synchronized drumming enhances 571
- activity in the caudate and facilitates prosocial commitment-if the rhythm comes easy. 572
- PloS one 6, e2727. 573
- Konvalinka, I., Vuust, P., Roepstorff, A. and Frith, C.D. 2010: Follow you, follow me: 574
- continuous mutual prediction and adaptation in joint tapping. Quarterly Journal of 575
- Experimental Psychology 63, 2220–2230. 576
- Koob, G.F. 1992: Drugs of abuse: anatomy, pharmacology and function of reward pathways. 577
- Trends in Pharmacological Sciences 13, 177–184. 578
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U. and Fehr, E. 2005: Oxytocin increases 579
- trust in humans. Nature 435, 673-676. 580
- 581 Kudo, H. and Dunbar, R.I.M. 2001: Neocortex size and social network size in primates.
- Animal Behaviour **62**, 711–722. 582
- Lakens, D. and Stel, M. 2011: If they move in sync, they must feel in sync: Movement 583
- 584 synchrony leads to attributions of rapport and entitativity. Social Cognition 29, 1–14.
- Launay, J. 2015a: Music as a technology for social bonding: Comment on' Music, empathy, 585
- and cultural understanding" by E. Clarke et al. Physics of Life Reviews 15-94. 586
- Launay, J. 2015b: Musical sounds, motor resonance and agency detection. Empirical 587
- Musicology Review 10, 30–40. 588

- Launay, J., Dean, R. and Bailes, F. 2013: Synchronization can influence trust following virtual interaction. Experimental Psychology **60**, 53–63.
- Launay, J., Dean, R.T. and Bailes, F. 2014: Synchronising movements with the sounds of a virtual partner enhances partner likeability. Cognitive Processing 15, 491–501.
- Lehmann, J., Korstjens, A.H. and Dunbar, R.I.M. 2007: Group size, grooming and social cohesion in primates. Animal Behaviour **74**, 1617–1629.
- Leknes, S. and Tracey, I. 2008: A common neurobiology for pain and pleasure. Nature Reviews Neuroscience **9**, 314–320.
- Lepage, C., Drolet, P., Girard, M., Grenier, Y. and DeGagné, R. 2001: Music decreases sedative requirements during spinal anesthesia. Anesthesia and analgesia **93**, 912–916.
- Levine, J.., Gordon, N.C. and Fields, H.L. 1979: Naltrexone dose dependently produces analgesia and hyperalgesia in postoperative pain. Nature **278**, 740–741.
- Lim, M.M. and Young, L.J. 2006: Neuropeptidergic regulation of affiliative behavior and social bonding in animals. Hormones and Behavior **50**, 506–517.
- Loh, H.H., Tseng, L.F., Wei, E. and Li, C.H. 1976: β-endorphin is a potent analgesic agent.

 Proceedings of the National Academy of Sciences, USA 73, 2895–2898.
- Lumsden, J., Miles, L.K., Richardson, M.J., Smith, C.A. and Macrae, C.N. 2012: Who syncs?
 Social motives and interpersonal coordination. Journal of Experimental Social
 Psychology 48, 746–751.
- Ma, Y., Liu, Y., Rand, D.G., Heatherton, T.F. and Han, S. 2015: Opposing oxytocin effects
 on intergroup cooperative behavior in intuitive and reflective minds.
 Neuropsychopharmacology 40, 2379–2387.
- Machin, A.J. and Dunbar, R.I.M. 2011: The brain opioid theory of social attachment: a review of the evidence. Behaviour **148**, 985–1025.
- Martel, F.L., Nevison, C.M., Simpson, M.J. and Keverne, E.B. 1995: Effects of opioid receptor blockade on the social behavior of rhesus monkeys living in large family groups. Developmental Psychobiology **28**, 71–84.
- McKinney, C.H., Tims, F.C., Kumar, a M. and Kumar, M. 1997: The effect of selected classical music and spontaneous imagery on plasma beta-endorphin. Journal of Behavioral Medicine **20**, 85–99.
- McNeill, W.H. 1995: Keeping Together in Time. Harvard University Press, Cambridge, MA, 620
- Meller, R.E., Keverne, E.B. and Herbert, J. 1980: Behavioural and endocrine effects of naltrexone in male talapoin monkeys. Pharmacology, Biochemistry, and Behavior 13,
- 623 663–672.

- Menon, V. and Levitin, D.J. 2005: The rewards of music listening: response and
- physiological connectivity of the mesolimbic system. NeuroImage **28**, 175–184.
- Merker, B. 2000: Synchronous chorusing and human origins. In Wallin, N., Merker, B. (eds.), The Origins of Music, 315–327. MIT Press, Cambridge, MA.
- Merker, B.H., Madison, G.S. and Eckerdal, P. 2009: On the role and origin of isochrony in human rhythmic entrainment. Cortex **45**, 4–17.
- 630 Miles, L.K., Nind, L.K. and Macrae, C.N. 2009: The rhythm of rapport: Interpersonal
- 631 synchrony and social perception. Journal of Experimental Social Psychology 45, 585–
- 632 589.
- 633 Miles, L.K., Griffiths, J.L., Richardson, M.J. and Macrae, C.N. 2010: Too late to coordinate:
- 634 Contextual influences on behavioral synchrony. European Journal of Social Psychology
- **40**, 52–60.
- 636 Miles, L.K., Lumsden, J., Richardson, M.J. and Macrae, C.N. 2011: Do birds of a feather
- move together? Group membership and behavioral synchrony. Experimental Brain
- 638 Research **211**, 495–503.
- 639 Mueller, C., Klega, A., Buchholz, H.-G., Rolke, R., Magerl, W., Schirrmacher, R.,
- Schirrmacher, E., Birklein, F., Treede, R.-D. and Schreckenberger, M. 2010: Basal
- opioid receptor binding is associated with differences in sensory perception in healthy
- human subjects: a [18F]diprenorphine PET study. NeuroImage **49**, 731–737.
- Nave, G., Camerer, C. and McCullough, M. 2015: Does oxytocin increase trust in humans? A critical review of research. Perspectives on Psychological Science **10**, 1–22.
- Nelson, E.E. and Panksepp, J. 1998: Brain substrates of infant-mother attachment:
- contributions of opioids, oxytocin, and norepinephrine. Neuroscience and Biobehavioral
- Reviews **22**, 437–452.
- Nilsson, U. 2008: The anxiety-and pain-reducing effects of music interventions: a systematic review. AORN Journal **87**, 780–807.
- Nilsson, U., Rawal, N., Enqvist, B. and Unosson, M. 2003: Analgesia following music and
- therapeutic suggestions in the PACU in ambulatory surgery; a randomized controlled
- trial. Acta anaesthesiologica Scandinavica 47, 278–283.
- Nilsson, U., Rawal, N., Uneståhl, L.E., Zetterberg, C. and Unosson, M. 2001: Improved
- recovery after music and therapeutic suggestions during general anaesthesia: a double-
- blind randomised controlled trial. Acta anaesthesiologica Scandinavica 45, 812–817.
- Nummenmaa, L., Tuominen, L., Dunbar, R.I.M., Hirvonen, J., Manninen, S., Arponen, E.,
- Machin, A., Hari, R., Jääskeläinen, I.P. & Sams, M. 2016: Reinforcing social bonds by
- touching modulates endogenous μ-opioid system activity in humans. NeuroImage.

- Oesch, N. and Dunbar, R.I.M. 2015: Influence of Kin Network on Maternal and Infant Health and Illness. Journal of Pregnancy and Child Health **2**, 146–156.
- Olmstead, M.C. and Franklin, K.B. 1997: The development of a conditioned place preference
- to morphine: effects of lesions of various CNS sites. Behavioral Neuroscience 111,
- 663 1313–1323.
- Oullier, O., de Guzman, G.C., Jantzen, K.J., Lagarde, J. and Kelso, J. a S. 2008: Social coordination dynamics: measuring human bonding. Social neuroscience **3**, 178–192.
- Panksepp, J. 1999: Affective Neuroscience. Oxford University Press, Oxford, .
- Pearce, E., Launay, J. and Dunbar, R.I.M. 2015: The ice-breaker effect: singing mediates fast social bonding. Royal Society Open Science. doi: 10.1098/rsos.150221
- Pearce, E., Mac Carron, P., Launay, J. and Dunbar, R.I.M. in press: Tuning in to others:
- Exploring relational and collective bonding in singing and non-singing groups over time.
- 671 Psychology of Music
- Pedersen, C.A. and Prange, A.J. 1979: Induction of maternal behavior in virgin rats after
- intracerebroventricular administration of oxytocin. Proceedings of the National
- Academy of Sciences of the United States of America **76**, 6661–6665.
- Reddish, P., Fischer, R. and Bulbulia, J. 2013: Let's dance together: synchrony, shared intentionality and cooperation. PloS one 8, e71182.
- Van Ree, J.M., Niesink, R.J., Van Wolfswinkel, L., Ramsey, N.F., Kornet, M.M., Van Furth,
- W.R., Vanderschuren, L.J., Gerrits, M.A. and Van den Berg, C.L. 2000: Endogenous
- opioids and reward. European Journal of Pharmacology **405**, 89–101.
- Rizzolatti, G. and Craighero, L. 2004: The mirror-neuron system. Annual Review of Neuroscience **27**, 169–192.
- Ryder, T.B., Blake, J.G., Parker, P.G. and Loiselle, B. a. 2011: The composition, stability,
- and kinship of reproductive coalitions in a lekking bird. Behavioral Ecology 22, 282–
- 684 290.
- Savaskan, E., Ehrhardt, R., Schulz, A., Walter, M. and Schächinger, H. 2008: Post-learning
- intranasal oxytocin modulates human memory for facial identity.
- Psychoneuroendocrinology **33**, 368–374.
- 688 Shamay-Tsoory, S.G., Abu-Akel, A., Palgi, S., Sulieman, R., Fischer-Shofty, M., Levkovitz,
- Y. and Decety, J. 2013: Giving peace a chance: oxytocin increases empathy to pain in
- the context of the Israeli–Palestinian conflict. Psychoneuroendocrinology **38**, 3139–
- 691 3144.
- Shultz, S., Opie, C. and Atkinson, Q.D. 2011: Stepwise evolution of stable sociality in
- 693 primates. Nature **479**, 219–222.
- 694 Silk, J.B. 2007: Social components of fitness in primate groups. Science 317, 1347–1351.

- 695 Silk, J.B., Alberts, S.C. and Altmann, J. 2003: Social Bonds of Female Baboons. Science 302, 1231–1235.
- 697 Stefano, G.B., Zhu, W., Cadet, P., Salamon, E. and Mantione, K.J. 2004: Music alters
- constitutively expressed opiate and cytokine processes in listeners. Medical science
- monitor: international medical journal of experimental and clinical research 10, MS18–
- 700 MS27.
- 701 Steinbeis, N. and Koelsch, S. 2009: Understanding the intentions behind man-made products
- elicits neural activity in areas dedicated to mental state attribution. Cerebral Cortex 19,
- 703 619–623.
- Sullivan, P.J. and Rickers, K. 2013: The effect of behavioral synchrony in groups of
- teammates and strangers. International Journal of Sport and Exercise Psychology 11,
- 706 286–291.
- Sullivan, P.J., Rickers, K. and Gammage, K. 2014: The effect of different phases of
- synchrony on pain threshold. Group Dynamics: Theory, Research and Practice 18, 122–
- 709 128.
- Sutcliffe, A., Dunbar, R., Binder, J. and Arrow, H. 2012: Relationships and the social brain:
- 711 integrating psychological and evolutionary perspectives. British Journal of Psychology
- **103**, 149–168.
- 713 Tarr, B., Launay, J., Cohen, E. and Dunbar, R.I.M. 2015: Synchrony and exertion during
- dance independently raise pain threshold and encourage social bonding. Biology Letters.
- 715 doi: 10.1098/rsbl.2015.0767
- 716 Tarr, B., Launay, J. and Dunbar, R.I., M.: 2016. Silent disco: dancing in synchrony leads to
- 717 elevated pain thresholds and social closeness. Evolution and Human Behavior. doi:
- 718 10.1016/j.evolhumbehav.2016.02.004
- 719 Trezza, V. and Vanderschuren, L.J.M.J. 2008: Bidirectional cannabinoid modulation of social
- behavior in adolescent rats. Psychopharmacology **197**, 217–227.
- 721 Tunçgenç, B., Cohen, E.E.A. and Fawcett, C. 2015: Rock with me: The role of action
- synchrony in infants' social and non-social choices. Child Development. doi:
- 723 10.1111/cdev.12354
- Van Ulzen, N.R., Lamoth, C.J.C., Daffertshofer, A., Semin, G.R. and Beek, P.J. 2008:
- 725 Characteristics of instructed and uninstructed interpersonal coordination while walking
- side-by-side. Neuroscience letters **432**, 88–93.
- Valdesolo, P. and Desteno, D. 2011: Synchrony and the social tuning of compassion.
- 728 Emotion 11, 262–266.
- Weinstein, D., Launay, J., Pearce, E., Dunbar, R.I.M. and Stewart, L. 2015: Music, pain
- thresholds, and social connections: the effect of singing in small and large groups.
- Evolution and Human Behavior. doi: doi: 10.1016/j.evolhumbehav.2015.10.002

- Wiltermuth, S.S. 2012: Synchronous activity boosts compliance with requests to aggress.
- Journal of Experimental Social Psychology **48**, 453–456.
- Wiltermuth, S.S. and Heath, C. 2009: Synchrony and cooperation. Psychological Science 20,
- 735 453–456.
- Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M. and Cheney, D.L.
- 737 2008: Focused grooming networks and stress alleviation in wild female baboons.
- 738 Hormones and Behavior **54**, 170–177.
- Young, L.J. and Wang, Z. 2004: The neurobiology of pair bonding. Nature Neuroscience 7,
- 740 1048–1054.
- Young, L.J., Lim, M.M., Gingrich, B. and Insel, T.R. 2001: Cellular mechanisms of social
- attachment. Hormones and Behavior **40**, 133–138.
- Zak, P.J., Kurzban, R. and Matzner, W.T. 2005: Oxytocin is associated with human
- trustworthiness. Hormones and behavior **48**, 522–527.
- Zak, P.J., Stanton, A.A. and Ahmadi, S. 2007: Oxytocin increases generosity in humans. PloS
- one 2, e1128.
- Zatorre, R.J., Chen, J.L. and Penhune, V.B. 2007: When the brain plays music: auditory-
- motor interactions in music perception and production. Nature Reviews. Neuroscience 8,
- 749 547–558.
- 750 Zillmann, D., Rockwell, S., Schweitzer, K. and Sundar, S.S. 1993: Does humor facilitate
- coping with physical discomfort? Motivation and Emotion 17, 1–21.
- Zubieta, J.K., Smith, Y.R., Bueller, J.A., Xu, Y., Kilbourn, M.R., Jewett, D.M., Meyer, C.R.,
- Koeppe, R. a and Stohler, C.S. 2001: Regional mu opioid receptor regulation of sensory
- and affective dimensions of pain. Science (New York, N.Y.) 293, 311–315.