

SMILE ASYMMETRIES AND REPUTATION AS RELIABLE INDICATORS OF LIKELIHOOD TO COOPERATE: AN EVOLUTIONARY ANALYSIS

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ABSTRACT

Cooperating with individuals whose altruism is not motivated by genuine prosocial emotions could have been costly in ancestral division of labour partnerships. How do humans 'know' whether or not an individual has the prosocial emotions committing future cooperation? Frank (1988) has hypothesized two pathways for altruist-detection: (a) facial expressions of emotions signalling character; and (b) gossip regarding the target individual's reputation. Detecting non-verbal cues signalling commitment to cooperate may be one way to avoid the costs of exploitation. Spontaneous smiles while cooperating may be reliable index cues because of the physiological constraints controlling the neural pathways mediating involuntary emotional expressions. Specifically, it is hypothesized that individuals whose help is mediated by a genuine sympathy will express involuntary smiles (which are observably different from posed smiles). To investigate this idea, 38 participants played dictator games (i.e. a unilateral resource allocation task) against cartoon faces with a benevolent emotional expression (i.e. concern furrows and smile). The faces were presented with information regarding reputation (e.g. descriptions of an altruistic character vs. a non-altruistic character). Half of the sample played against icons with symmetrical smiles (representing a spontaneous smile) while the other half played against asymmetrically smiling icons (representing a posed smile). Icons described as having altruistic motives received more resources than icons described as self-interested helpers. Faces with symmetrical smiles received more resources than faces with asymmetrical smiles. These results suggest that reputation and smile asymmetry influence the likelihood of cooperation and thus may be reliable cues to altruism. These cues may allow for altruists to garner more resources in division of labour situations.

How can genetic self-promotion design costly organism-level adaptations for delivering benefits to others? Simply put, how did altruism between non-kin evolve in humans? One adaptive problem for designing psychological adaptations mediating altruism is the costs associated with free-rider exploitation in division of labour partnerships. Imagine that you engage in a joint venture where you and your partner are task specialists reaping the benefits from your division of labour. Benefits are attained because neither of you would have been able to succeed at the goal without the other. However, if you chose your partner based on some arbitrary criteria (e.g. he or she told you “I am honest, you can trust me.”) you could be opening yourself up to exploitation. What compounds the costs of exploitation in a division of labour situation is that it is difficult to monitor cheating. Indeed in some conditions you may not even recognize cheating because you are not specialized in the task being performed.

One hypothesis for the maintenance of altruism in division of labour situations is that altruists encode subtle nonverbal cues signalling willingness to cooperate in the future (Frank, 1988). These signals are hypothesized to manipulate the sensory systems of other altruists, facilitating the formation of a coalition with the sender. If altruists can detect one another and form social support networks, this may allow for the selection of genes predisposing altruism. In mathematical simulations and modelling it appears that alliance formation among altruists cognitively equipped to detect one another may evolve (Frank, 1988; Peck, 1995; Wilson & Dugatkin, 1997; Cooper & Wallace, 1998; de Vos, Smaniotto, & Elsas, 2001). Surprisingly there is little evidence testing the basic assumption that humans can detect altruists (Brown & Moore, 2000). Furthermore even if altruists are detectable, how is this accomplished (e.g. what are the nonverbal and paralinguistic signals involved, and what are the costs maintaining signal reliability)? Despite the theoretical importance of reliable signals indicating altruistic character, to date no studies have isolated the signals or even demonstrated costs maintaining signal reliability.

This chapter has two goals. One is to integrate the literature on human altruism detection (i.e. Frank, 1988; Wilson & Dugatkin, 1997; Brown & Moore, 2000) with the field on animal signalling (Zahavi, 1987; Grafen, 1990; Adams & Mesterton-Gibbons, 1995; Guilford & Dawkins, 1995; Maynard Smith & Harper, 1988; 1995; Maynard Smith, 1991; Vehrencamp, 2000). The second goal is to report an experimental investigation of two potential signals of altruism (i.e. nonverbal and reputation cues). Both nonverbal and reputation cues to altruism have been hypothesized to maintain human cooperation via indirect reciprocity (Alexander, 1987; Hirshleifer, 1987; Frank, 1988) and multilevel selection processes (Wilson & Dugatkin, 1997). However, there is little experimental evidence supporting the hypothesis that reputation cues (e.g. being known as having sincere motives for helping others) and/or nonverbal expression of prosocial emotions lead to any tangible benefits. Section II of this chapter presents findings consistent with the hypothesis that nonverbal and reputation cues accrue tangible benefits in evolutionary games.

I. RELIABLE SIGNALLING THEORY AND HUMAN ALTRUIST-DETECTION

Prosocial emotion scrutiny would do well evolutionarily as altruism that is performed without a sympathetic basis would be less likely to occur again in the future when it is not in the self-interest of the individual (Trivers, 1971). That is, when help is motivated by self-interest (e.g. conscious concerns of reciprocity) the donor may not perform future acts of altruism when they are not being watched. Indeed, if prosocial emotions compel altruists to cooperate it is possible that self-interested emotions also compel individuals to cooperate only when it obviously benefits the donor. One problem of coordinating cooperating partnerships is determining the likelihood that a potential partner will cooperate in the future and do so even when not being monitored. Hirshleifer (1987) and Frank (1987) have provided detailed models extending Trivers' (1971) speculations on reliable indicators of future altruism. Specifically, the prosocial emotions are viewed as guarantees or commitment devices of future altruistic behaviour. The key to Frank's (1988) and Hirshleifer's (1987) models is that the emotions, which guarantee cooperative moves, can be reliably discerned (Zahavi, 1987; Grafen, 1990). How can perceivers reliably discern prosocial emotions? Ekman (1985) has reviewed the literature on nonverbal communication and suggests that body language, pitch and timbre of the voice, and facial expression can be reliable indicators of underlying affective states. Since the linkages from emotional states to the expression of these states are under involuntary control, perceivers may be exposed to reliable signals. Specifically, for mimics the costs of putting involuntary neural pathways and facial muscles under conscious control may be too costly (in terms of practice and/or re-configuring the physiology involved in the putative signals).

Nonverbal signals of prosociality are only reliable indicators of underlying altruistic intent when there are sender and/or receiver-imposed costs (Frank, 1988; Adams & Mesterton-Gibbons, 1995; Guilford & Dawkins, 1995; Brown & Moore, 2000). For example, when signals are cheap to fake mimics should proliferate and drive a population of honest signallers towards extinction. However, when mimics are unable to fake the signal, honest signallers can continue to transmit accurate information. Therefore if altruism is signalled nonverbally in humans, there must be some mechanism maintaining signal reliability. Indeed, selfish and/or deceptive mutants are a general problem for evolutionary models of cooperation and signalling (Michod & Roze, 2001).

Index and Conventional Cues to Human Altruism

A reliable signal is a cue that honestly reveals an aspect of the sender to one or more receivers. Why should animals (including humans) ever reveal anything about

themselves? There appears to be a number of conditions in which reliable signals can evolve when there are sender and receiver-imposed costs (see Table 1).

Table 1. Types of signals, costs, design and applications to human altruism (modified from Vehrencamp, 2000).

Signal Type	Costs	Signal Design	Application to Human Altruism
Index	Physiological / physical constraints	Signal design linked to sender attributes	Neural mechanisms controlling involuntary expression of prosocial emotions (e.g. smiling).
Quality Handicap	Signal production	Signal intensity linked to sender quality	Social status and/or capacity to cooperate.
General Handicap	Signal production	Signal intensity linked to sender need	How much one needs assistance from others.
Vulnerability Handicap	Vulnerability to receiver attack	Signal places sender at risk of receiver attack	Signalling willingness to cooperate may attract exploiters.
Conventional	Receiver retaliation	Arbitrary form	Punishment of deceptive signalers allows for signal reliability.

As seen in Table 1, the primary literature on animal signalling focuses on five ways in which reliable signals are costly (Vehrencamp, 2000). These types of reliable signals can be divided into those signals that impose a cost on the sender (e.g. signal production costs like bright, parasite free, tail feathers) and signals that impose costs due to the receiver's behaviour in response to the signal (Adams & Mesterton-Gibbons, 1995; Guilford & Dawkins, 1995). Specifically, the signal may have costs inflicted upon the sender by the receiver (i.e. receiver-dependent costs) or imposed by the sender's signal itself (i.e. sender-dependent costs). Either way the signal will be reliable as long as there are costs preventing deceit. There may be two distinct types of sender-dependent costs: (a) physiological constraints preventing mimicry (i.e. "index signals"); and (b) signal production costs (signal is a costly handicap for survival). There are two sub-types of handicaps with sender-dependent costs. One is when signal production correlates with sender genetic quality (e.g. Peacock's tail) and the other is when signal production is correlated with sender's need for assistance (e.g. hunger or thirst). Examples of two distinct types of receiver-dependent costs are: (a) signal increases likelihood of receiver attacking the sender; and (b) receivers punish mimics. Table 1 also highlights the ways in which theoretical findings on animal signalling may inform evolutionary psychologists interested in signals of altruism. In the fourth column of Table 1 the application to human

altruism is briefly described. For example, the neural mechanisms controlling involuntary facial expressions of prosocial emotions (e.g. concern and interest for others) may qualify as a reliable index signal (this will be discussed in more detail in the section entitled “Index Cues to Human Altruism”). With the index signal there are no costs to signal production, only to signal mimicry. Quality handicaps may be connected to human altruism signalling. Analogous to the peacock’s tail, individuals who have high social status may bestow altruism upon others (Zahavi, 1987). This could increase the donor’s status and/or mating opportunities (Boone, 1998). General handicaps may assist signal reliability in human cooperative ventures. Specifically, signals of need may reflect the degree to which donors require assistance. The Sir Philip Sidney game has been used to model how signals of need are evolutionarily stable (Maynard Smith, 1991). Regardless of the importance of reliable signals of need in evolutionary games, the reliability of signals of altruism may be an orthogonal issue. Vulnerability handicaps may have more relevance for altruism signals in humans. Individuals that signal altruistic intentions may be revealing to exploiters that they are ideal ‘suckers’ in division of labour partnerships. Only individuals capable of buffering the costs of exploitation may bother signalling cooperative intentions. One example of a buffering capacity may be if the altruist has a large kin/and or non-kin group capable of retaliating on the donor’s behalf. The final signal type in Table 1 is the conventional signal. In the case of human altruism any signal (e.g. verbal promises) could potentially become associated with likelihood to be altruistic. If mimics adopt the signal there may be high receiver retaliation costs (e.g. punishment) for not following through with the promise of cooperation.

Of course prosocial emotion signalling may potentially fall into any of the five signal types - see Table 1. This chapter investigates the possibility of physiologically constrained index signals and conventional signals of altruism. The reason for this focus is that there is evidence in the field of cognitive neuroscience that spontaneous (i.e. ‘heartfelt’) emotional expressions are physiologically constrained via dedicated neural pathways (Gazzaniga, Ivry, & Mangun, 1998). The second type of reliable signal focused upon in this chapter is the conventional signal. A conventional signal in the case of human altruism signalling would be when deceptive signallers lie that they are altruistic (e.g. via language). In this case deceptive information may be heavily punished by perceivers when the convention is violated (i.e. not lying about your willingness to engage in unselfishly motivated acts of altruism).

Index Cues to Human Altruism

For a cue to altruism to qualify as an index the signal would have to be physiologically constrained (Maynard Smith & Harper, 1988; 1995; Maynard Smith, 1991; Vehrencamp, 2000). Physiologically constrained cues prevent signal mimicry. For example, some forms of nonverbal display could qualify as index signals if they were reliably linked to likelihood of future altruism. Although it should be reminded that no nonverbal configuration of signals has been shown to be reliably linked to human altruism. One possibility for an altruism / facial expression link is the human smile.

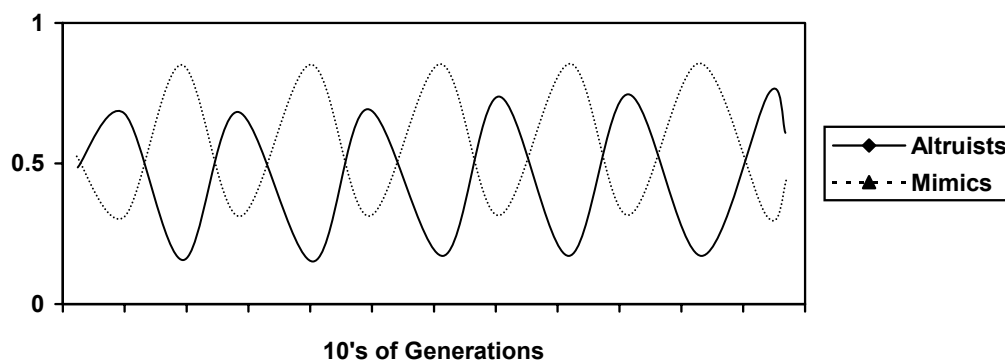
In humans, the smile is under the control of two neural pathways (Meihlke, 1973; Myers, 1976; Ekman, Hage & Friesen, 1981; Wylie & Goodale, 1988; Gazzaniga & Smylie, 1990; Smith, Smith, & Ellgring, 1996; Gazzaniga, Ivry, & Mangun, 1998). One pathway mediates spontaneous smiling expressions and may be implicated in unfakeable prosocial signals. Due to neuro-architectural constraints on spontaneous smiles (e.g. see Gazzaniga & Smylie, 1990) an individual's self-interested tendencies may be detected before they cheat. For example when conditions require a target to perform (or return) a favour their facial expressions will be scrutinized. If a cooperater produces 'half-hearted' facial expressions (e.g. a phoney smile) in the context of helping others, the receivers of these cues may conclude that the target lacks the prosocial motivation to help. Alternatively, when genuine altruists are required to perform (or return) a favour their facial expressions should appear more genuine and interested in helping. A good example of a facial expression constrained by neural pathways is 'genuine' and 'false' smile (Ekman & Friesen, 1982; Gazzaniga & Smylie, 1990). When helping, prosocial targets should smile more genuinely than antisocial targets.

However, due to the payoffs for deceptive signals, perfect altruist-detection may not be expected unless the costs of scrutiny are amply repaid (e.g. via the formation of altruist-altruist partnerships). Specifically, when the costs of exploitation are high and the probability of interacting with an exploiter is high, computational energy requirements for detection should be paid to receive the benefits of trustworthy division of labour partnerships. In the following paragraphs a hypothesized frequency-dependent arms race between deception and deception-detection is elucidated.

Perfectly distinguishable signals of altruism suffer from a fatal conceptual flaw as pointed out by Frank (1988). Imagine a population where the signal for altruism was an easily recognizable "A" on the sender's forehead. Over evolutionary time cooperators will assortate leaving defectors to interact with one another. The frequency of defectors should gradually disappear from the population. In this type of ecology there would be large fitness benefits to signal mimicry. If physiological mimicry were possible natural selection would favour it and altruists would begin to interact randomly. From the point of view of altruists the costs of random interaction depends upon the frequency of defectors in the population (which would be increasing due to added benefits of exploiting others cooperative efforts).

Since the benefits of deception are great when deceivers are at low frequency (Frank, 1988), it is expected that natural selection may favour re-configuring neural pathways to avoid detection. Counter adaptations to avoid deception-detection may select for once spontaneous expressions to come under voluntary control. Therefore altruism signals lose reliability. All other things being equal, once prosocial signals fail to maintain reliability, altruists (or signalling intentions) should decrease in frequency. When deceivers are able to mimic prosocial signals (e.g. via mutation) they should increase in frequency in a population, which in turn may select for receivers who will punish or avoid misleading signals. It should be pointed out that signalling and mimicry of altruistic emotions may resemble a predator-prey arms race.

Figure 1. A frequency-dependent polymorphism whereby mimics and altruists are fluctuating around equilibrium point over evolutionary time.



As seen in Figure 1 when the frequency of altruists is high there will be a niche for deceptive communication. This is due to altruists not bothering to pay the costs of scrutiny (e.g. time and effort to decode signal – see Frank, 1988) when the probability of interacting with another altruist is high. Once mimics master the signal, altruists will begin to decrease in the population (relative to mimics). However, mimics do not have a monopoly on evolving effective counter-adaptations. As soon as the signal becomes meaningless altruists could begin discriminating intentions based on some other cue – thus increasing in frequency via assortative interactions once again. Frank’s (1988) model predicts that there have been frequency-dependent oscillations between signal detection and signal deception over evolutionary time. Trivers’ (1985) also has an interesting discussion of this hypothesized arms race between deception and deception-detection.

Conventional Cues to Human Altruism

Another pathway for the formation of altruist-altruist partnerships is basing assessments on conventional signals of altruistic reputation. Reputations for honesty are important in humans cross-culturally (Brown, 1991). Alexander (1988) pointed to the benefit of indirect reciprocity whereby individuals cultivate a reputation for altruism among third party reciprocators. For example helping the sick or elderly who cannot reciprocate could facilitate third party altruism directed towards the donor. In order for an altruistic reputation to be a conventional signal there must be punishment of individuals who foster an altruistic reputation as they subtly cheat others. Cooperating for the preview of others may not be sufficient to cultivate an altruistic reputation. Rather helping others with an emotional regard for the recipient’s interest may be a crucial

criterion for receivers to deliver third party benefits in human societies (Brown & Moore, 2000). Frank's (1988) model of human altruism assumes that there are costs to signal scrutiny and they may not be paid unless the probability of interacting with a cheater in division of labour situations is high. It is reasonable to predict that there are cues to altruism and that in evolutionary environments these cues would be heavily scrutinized in order to make reliable partner selections due to the costs of exploitation. In the next section smile asymmetries and reputation are empirically explored.

II. INVESTIGATION OF SMILE ASYMMETRY AND REPUTATION CUES

There have been few studies on what aspects of facial expression may cue others to an individual's level of altruism. Based on theoretical work discussed in the first part of this chapter it would be expected that smile asymmetries and reputation might be reliable cues to underlying altruistic intent.

Smiling - A Reliable Index Cue to Altruism?

Neuroscience has investigated the physiological constraints on the human smile (Meihlke, 1973; Myers, 1976; Ekman, Hage & Friesen, 1981; Wylie & Goodale, 1988; Gazzaniga & Smylie, 1990; Smith, Smith, & Ellgring, 1996; Gazzaniga, Ivry, & Mangun, 1998). Most of this work does not explicitly have an evolutionary point of view and has never considered the possibility that the smile may reliably signal aspects of character or intentions.

As discussed in Section I humans have two neural systems for controlling smiles: one under involuntary control and the other under voluntary control (Gazzaniga & Smylie, 1990; Gazzaniga, Ivry, & Mangun, 1998). The left hemisphere of the brain has been found to control voluntary smiles (Gazzaniga & Smylie, 1990). The left-side of the brain sends messages to the contralateral VII nucleus which then innervates the facial muscles on the right side of the face (Gazzaniga & Smylie, 1990). Simultaneously, the left hemisphere also sends information across the corpus callosum to the right hemisphere, which functions to innervate the facial muscles on the left-side of the face. This only occurs during posed, voluntary smiles. Wylie and Goodale (1988) have shown that posed smiles are asymmetrical (i.e. the right-side is higher than the left-side of the mouth).

For spontaneous or involuntary smiles a different neural pathway is involved. In contrast to posed smiles (which are only triggered by the left hemisphere) spontaneous smiles can be triggered by both hemispheres. When an individual experiences a spontaneous emotion, a signal travels directly through the midbrain to the brainstem nuclei, bypassing the cortex (Gazzaniga et al., 1998). Both hemispheres send signals directly down through the midbrain to the brainstem nuclei.

Further evidence for two neural pathways in smiling comes from lesion studies. Specific lesions in the pyramidal system can impair an individual's ability to smile on request, but the same person can smile normally if amused (Meihlke, 1973; Myers, 1976). The reverse is true for other neurological disorders, such as Parkinson's disease. In Parkinson's disease the patient cannot spontaneously smile when happy but can produce a posed smile upon request (Smith, Smith, & Ellgring, 1996).

When humans experience pleasure they spontaneously smile and the left side of the smile shows more displacement than the right side (Wylie & Goodale, 1988). Wylie and Goodale (1988), in a controlled study measuring smile asymmetries found that during a spontaneous smile, the left-side of the mouth is more displaced than in a posed smile. Strobe cameras and computer analysis of reference points on the corners of the mouth revealed that the left side of the mouth moved more in spontaneous than posed smiles in the same targets. This indicates that the right hemisphere is more involved in spontaneous emotional expression as compared to the left hemisphere. Not surprisingly humans scrutinize the left side of the face more than the right side when assessing facial expressions (Burt & Perret, 1997).

Since there are different neural pathways and observable differences between spontaneous and posed smiling behaviour in humans it is possible that perceivers will scrutinize smile asymmetries in cooperative situations to make assessments regarding genuine concern for others.

Adaptive Benefits to the Human Smile?

Is there evidence that the human smile is a signal of trust or altruism? Research suggests that humans trust smiling individuals more than non-smiling individuals (Otta, Lira, Delevati, Cesar & Pires, 1994; Lafrance & Hecht, 1995). Specifically smiling newscasters can influence political candidate choice (Mullen et al., 1986). Interestingly in 50 randomly collected photographs of George W. Bush and Al Gore taken during the USA's 2000 Presidential race, Bush produced significantly more genuine smiles (Brown & Moore, unpublished data). According to a Gallup poll (www.gallup.com) before Election Day, Bush was rated as more sincere and trustworthy than Al Gore. Recent experimental work shows that photographs of smiling individuals are trusted more than non-smiling individuals (Schalemann, Eckel, Kacelnik, & Wilson, In Press). The human smile is expressed in social situations and could be viewed as a revealer of underlying intentions. For example, if an individual is smiling while helping others, perceivers may assume that the smiling person is in fact genuinely motivated to help. However, natural selection should discourage simply assuming that a smiling individual is trustworthy. Specifically, a con artist could easily put on a false smile while helping and trick perceivers into trusting him or her. Perhaps natural selection has favoured skeptical perceivers who scrutinize smiles according to asymmetry. This would only be the case if smile asymmetries were reliable indicators of underlying emotional states.

Reputation Cues

In order for an altruistic reputation to function as a conventional signal there must be some way to penalize deception. Two possible costs to the development of an altruistic reputation are: (a) The time and effort required performing unreciprocated altruistic acts for the preview of others; and (b) Punishment for the deceptive boasting of how altruistic one is when in fact they are not altruistic. One would expect information regarding an altruistic character to influence resource allocations. Previous empirical findings (i.e. Brown & Moore, 2000) using a different research paradigm (i.e. the Wason selection task) found that subjects could detect genuine altruism. It appears that information-processing mechanisms for altruist-detection are designed in such a way to scrutinize the underlying motivations for helping (i.e. self-interested vs. other-interested helping).

Detecting motivations for helping may sometimes occur through word of mouth or gossip (Alexander, 1987; Frank, 1988). Individuals between and within social groups may exchange information regarding an individual's motives for helping in the past. Forming a consensus about a person's ability to be trusted may be beneficial and be involved in indirect reciprocity (Alexander, 1987; Nowak & Sigmund, 1998). Repeated altruistic acts mediated by a concern for the recipient contribute to an altruistic reputation being bestowed upon the altruist by others. When character assessments by multiple individuals (with unique perspectives and/or sensory capacities) are involved in formation of an altruistic reputation, then reputation may help decrease the costs associated with individual scrutiny. Essentially, such a system of altruist-detection would be analogous to mate-choice copying in sexual selection models. That is, if everyone trusts individual 'x' then it may pay to befriend that individual since they are likely altruistic. However, this system could be vulnerable to cheats due to an initially poor assessment that is subsequently copied by others indiscriminately. As well some individuals may not pay the costs associated with detection and reap the benefits of other's scrutiny. Therefore, facial expressions may still be the most reliable way to assess an altruistic character.

Current Study

To explore the idea that humans assess smiles and reputation in cooperative contexts, these properties were varied in an experiment in which participants played resource allocation games. Icons exhibiting different types of smiles (asymmetrical smile vs. symmetrical smile) were presented to participants along with information regarding the intentions of icons (e.g. selfish vs. altruistic). Cartoon icons representing particular stylized emotions have been used in numerous psychology experiments (Hansen & Hansen, 1988; Hoptman & Levy, 1988; Yeo et al., 1997). Icons are an effective way to control for extraneous features of the human face that are unrelated to the emotion under investigation. In order to stylistically represent the emotion of prosocial concern two aspects of the cartoon face (i.e. eyebrow concern furrows and smiles) were selected due the evidence suggesting that these expressions are cross-cultural signals of affiliation

(Grant, 1969; Tidd & Lockard, 1978; Eibl-Eibesfeldt, 1989). The symmetrically smiling icon was used to represent a genuine, involuntary smile. An asymmetrically smiling icon (see Figure 2) was used to represent a posed, voluntary smile.

The dictator game was selected as a measure of subjects' resource allocations because it is widely used in experimental economics as a test of cooperative tendencies in humans (Eckel & Grossman, 1996; Bolton, Katok, & Zwick, 1998; Andreoni & Vesterlund, 2001). The dictator game is an unilateral resource allocation game that requires subjects to divide a valued resource between themselves and an opponent (Eckel & Grossman, 1996). In dictator games the experimenter asks subjects to divide up a resource (e.g. money) between themselves and another individual. It was predicted that participants would deliver fewer resources in dictator games to selfishly motivated icons and icons with asymmetrical smiles.

METHODS

Participants:

Thirty-eight (female $n = 22$; male $n = 16$) Introductory Psychology students (mean age = 20.08; $SD = 4.10$) participated for 1% credit toward class grade.

Procedure:

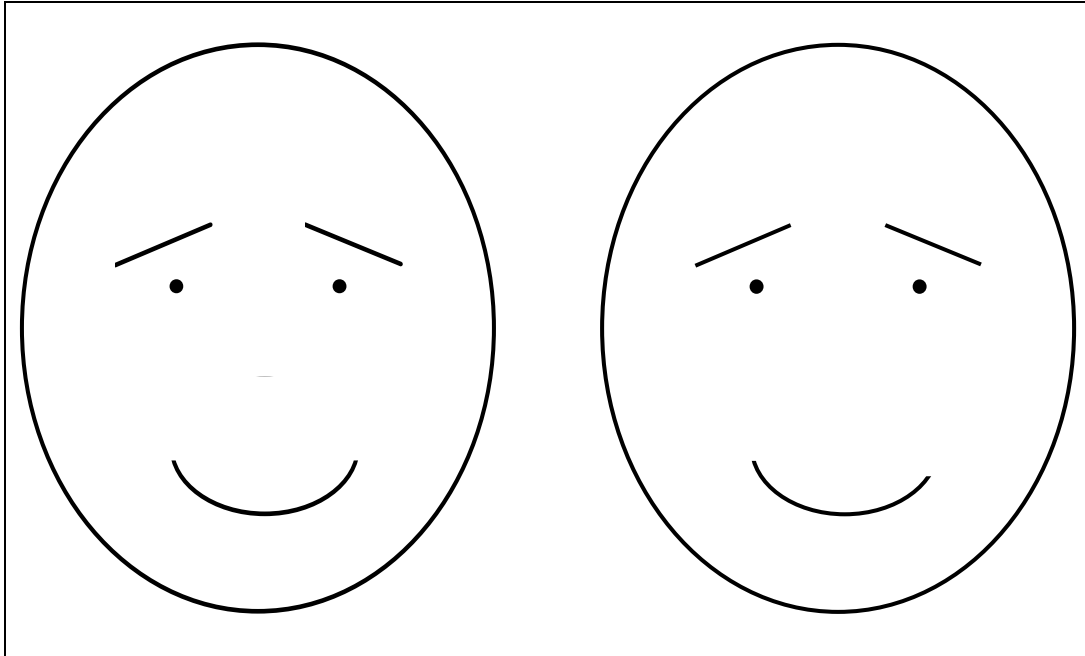
After signing consent forms, participants played one-shot dictator games for a valued resource against cartoon icons. The valued resources in this experiment were lottery tickets for a cash draw (total value of prizes = \$120). Specifically subjects divided 20 tickets between themselves and a cartoon icon. In addition, subjects were asked to predict how many tickets they believed the icon would give them. Each participant played against two icons; one described as a self-interested cooperator and one described as an altruistic cooperator. Finally, half of the sample ($n = 19$) played against symmetrically smiling icons and the other half ($n = 19$) played asymmetrically smiling icons. Participants were naive with respect to this between-subjects manipulation.

Manipulation of Smile Asymmetry:

Smile symmetry was manipulated only on the left-side of the face in accordance with the neuropsychological literature that suggests this is one difference between posed and spontaneous smiles (Meihlke, 1973; Myers, 1976; Ekman, Hage & Friesen, 1981; Wylie & Goodale, 1988; Gazzaniga & Smylie, 1990; Smith, Smith, & Ellgring, 1996; Gazzaniga, Ivry, & Mangun, 1998). Figure 2 depicts an example of the cartoon icons used in Study Two (symmetrical smile vs. asymmetrical smile). The asymmetrical smile

represents the posed false smile, while the symmetrical smile is designed to represent a genuine felt smile.

Figure 2. Benevolent icons with symmetrical and asymmetrical versions of the smile.



Manipulation of altruistic reputation: Each icon had either a reputation for altruism or self-interest. The descriptions were taken from Brown and Moore's (2000) altruist-detection Wason task. Their altruist-detection tasks were based on Trivers' (1971) hypothesis that natural selection should have designed perceiver psychological mechanisms to scrutinize whether motives of generosity accompany the altruistic act, since such forms of altruism would be more likely to occur in the future. Therefore the altruistic motive for the helping condition stated, "Gave blood and refused cash reward" while the self-interested motives for helping condition stated, "Gave blood and demanded cash reward."

RESULTS

Reciprocity Based Decision-Making

As expected, the number of tickets players thought they would receive was significantly and positively correlated with the number of tickets they gave to the icons:

[$R = .67$, $F(1, 36) = 29.63$, $p = .001$]. This is what would be expected if the decision rules mediating human cooperation were based upon reciprocity.

Assessments: Smile Asymmetry and Reputation Effects

The number of tickets perceivers predicted icons would allocate was analyzed using an analysis of variance (ANOVA) with smile symmetry (asymmetrical smile vs. symmetrical smile) as a between-subjects factor and reputation (altruistic vs. self-interested) as a within-subjects factor. Players predicted that symmetrically smiling icons would give more tickets ($M = 10.80$ / $SD = 3.60$) than asymmetrically smiling icons ($M = 8.00$ / $SD = 3.60$): $F(1,36) = 5.05$, $p < .05$. In addition players predicted that icons described as altruistic in the past would give more tickets ($M = 13.60$ / $SD = 6.40$) than icons described only as self-interested helpers ($M = 5.60$ / $SD = 4.40$): $F(1,36) = 19.30$, $p < .001$. The interaction was not significant.

Resource Allocations: Smile Asymmetry and Reputation Effects

Number of tickets allocated was analyzed using an analysis of variance (ANOVA) with smile symmetry (asymmetrical smile vs. symmetrical smile) as a between-subjects factor and reputation (altruistic vs. self-interested) as a within-subjects factor. Symmetrically smiling icons received 9.60 tickets ($SD = 4.40$) while asymmetrically smiling icons received 6.80 tickets ($SD = 2.48$). This mean difference was significant: $F(1,36) = 5.05$, $p < .05$. In addition icons with altruistic reputations received more tickets ($M = 10.00$ / $SD = 5.20$) compared to icons with reputations for self-interested pseudo-altruism ($M = 6.00$ / $SD = 4.00$): $F(1,34) = 39.60$, $p < .001$. The interaction was not significant.

DISCUSSION

Consistent with predictions, smile symmetry and a reputation for altruistically motivated helping influenced game players' assessments of icons and resource allocations to icons. Specifically, icons that possessed symmetrical smiles received more resources compared to icons with asymmetrical smiles. An altruistic reputation influenced subjects' resource allocations. That is, icons with altruistic motives received more resources than icons described as self-interested helpers. Results suggest that smile asymmetry and reputation are scrutinized when deciding how to allocate resources. Consistent with reciprocal altruism theory (Trivers, 1971) game players were reciprocally minded. Based on reputation and facial expressions, game players anticipated cooperative moves prospectively and engaged in 'reciprocity' (i.e. game players gave more lottery tickets to icons they believed would give more lottery tickets to them).

Reputation Signals

Icons with information suggesting they were benevolent helpers in the past received more resources than icons described as being self-interested helpers. This result is consistent with the idea that a reputation for other-interested helping may be beneficial in evolutionary games. An altruistic reputation accounted for a substantial proportion of the variance in resource allocations (35 percent of the variance). Indeed this is more than smile asymmetry's influence upon resource allocations (14 percent of the variance). However, it should be pointed out that the smile asymmetry manipulation was implemented using a between-subjects rather than within-subjects design. Removing variance due to differences between subjects from the error variance greatly increases the power of within-subjects significance tests. Therefore, within-subjects designs are almost always more powerful than between-subject designs. Also, there may have been demand characteristics in the within-subjects manipulation of reputation increasing the putative effect size. Specifically, all subjects received icons with a description of an altruistic and selfish cooperator. Thus participants may have 'realized' what the experimenter was hypothesizing. Nevertheless, it appears that an altruistic reputation influences subjects' resource allocations. If this result holds up in more naturalistic conditions then one may assume that it would pay for altruists to cultivate a prosocial image.

Evolutionarily it is interesting to ask how difficult is for a con artist to cultivate a reputation for honesty. Con artists' evolutionary success at manipulating others may depend upon gossip. That is, the con must keep ahead of social transmission (Dugatkin, 1992). The critical factor appears to be the speed with which a con can infiltrate a group before his or her reputation. Research is needed to measure the speed of between-group information exchange relative to the speed of which a con artist can garner the interests of strangers between groups. It would be predicted that the relative difference should correlate with the frequency of con artists in a population.

Smiles as Index Signals

Previous research suggests that smiling individuals are trusted and receive more resources compared to non-smiling individuals (Tidd & Lockard, 1978; Otto et al., 1994; LaFrance & Hecht, 1995; Scharlemann et al., In Press). Cross-cultural ethological research by Eibl-Eibesfeldt (1989) suggests that smiles are affiliative signals. If others scrutinize smiles in order to assess trustworthiness it is expected that altruists would exhibit a left-biased smile asymmetry in social encounters.

Deception may have been a powerful selective force on early hominid cognition (Trivers, 1985; Trivers, 2000). Indeed if a particular pattern of smiling while helping others is believed by others to be signal of altruism one may expect natural selection to favour deceivers that could manifest the signal. Selection would most likely not favour

deceivers who practiced putting involuntary neural machinery and facial musculature under conscious control, since there may be high costs for being caught. However, a reversal in cerebral lateralization could accomplish a similar end product without the time, effort and risks associated with practice. If over the course of hominid evolution there was a mutation reversing hemispheric involvement in posed smiles, deceivers could prosper. For example, left-handers manifest posed smiles that have the characteristic left-sided oral asymmetry characteristic of a right-handers genuine or spontaneous smile (Wylie & Goodale, 1988). Deceivers may benefit from left-handedness since their posed smiles when helping could be misperceived as trustworthy. If this were true it would be expected that exploitative individuals would be more likely to be left-handed than right-handed since perceivers would have a difficult time detecting self-interest from the smile. In fact, criminal behaviour appears to vary with handedness. Specifically, more left-handers than right-handers have been involved in criminal acts (Coren, 1998). Interestingly in another study left-handers report themselves as being more manipulative and Machiavellian (Coren, 1994). Finally, there appears to be a correlation between psychopathy and handedness (Hare & Forth, 1985). Further research needs to explore the connection between cerebral asymmetries, facial expression and deception.

Finally, it should be noted that there are numerous candidates for reliable signals associated with altruism in human facial expression besides smile asymmetries. For example the orbicularis oculi (i.e. periocular muscle region) and the zygomaticus major or cheek muscle regions (Ekman & Freisen, 1982; Surakka & Hietanen, 1998) are also involved in the involuntary expression of emotions. Evolutionarily one may expect that if a deceiver entered the population with a genuine-looking phony smile, perceivers may be selected to scrutinize the eye region to make more reliable judgments regarding intentions. Viewing facial expression as a step-wise co-evolutionary arms race between signalers and perceivers may be a fruitful way to formulate hypotheses. Selection may adjust one region of facial expression in favour of deception, but this will create counter-selection pressures for perceivers to assess another uncorrelated region to ensure reliable detection.

In Dugatkin's (1992) model of the evolution of the con artist, deceivers prosper when they move from community to community faster than cultural transmission (i.e. gossip). Signaling trustworthiness nonverbally can benefit the con temporarily but eventually gossip may travel faster than they are able to migrate. Perhaps the best strategy for a Machiavellian con artist is to move from patch to patch quickly before cultural transmission can catch up to them. Cultural transmission of information regarding trust could travel particularly fast considering that humans appear to pay special attention to the motives underlying altruism (Brown & Moore, 2000). According to Alexander (1987) and Nowak and Sigmund (1998) humans assess the altruistic behaviour performed for the benefit of a third party. If the third party observer returns the benefits, cooperation could have evolved via indirect return payment. This is known as indirect reciprocity (Alexander, 1987). If perceivers assess nonverbal signals of prosocial emotions and rely on gossip between- and within-groups, exploiters could be at a disadvantage. Con artists most likely have evolved counter-strategies to avoid detection. Costs of scrutiny and frequency-dependent selection may be one route for the evolutionary maintenance of

deception (Frank, 1988). Perceivers may not bother scrutinizing intentions (which takes a lot of time and effort) when the frequency of altruists is high in population. Under these conditions con artists may prosper.

Limitations

Since resource allocations by game players were influenced by smile asymmetry it may be that the smile is a reliable index cue to altruistic intentions. This result should be viewed as preliminary. For instance the smile symmetry findings were based on cartoon icons that are not ecologically valid faces. Humans evolved to assess actual human faces, three dimensionally and in real time. In addition, perhaps any facial asymmetry (e.g. in the eyes, nostrils etc.) would elicit fewer resources allocated. Future research needs to use photographic quality stimuli with several facial features morphed asymmetrically to ensure that smile asymmetry per se is a cue to underlying self-interested intentions. Despite the limitations to the current study it is encouraging that in an ethological investigation of altruists and non-altruists playing a cooperative game, altruists appear to produce the left-sided bias when smiling (Brown, 1998).

Conclusions

Several evolutionary models have suggested that social network formation may be a pathway to the evolution and stability of cooperation (Frank, 1988; Peck, 1995; Wilson & Dugatkin, 1997). The research here suggests that humans assess altruism and preferentially deliver resources to altruists. Indeed, these assessments of altruism may be involved with the formation of social support networks. This is what an evolutionary approach would predict considering the ancestral fitness costs associated with unreciprocated altruism.

Honest signals with a reliable emotional basis may be needed to guarantee perceivers that the target is not a con artist. The burgeoning literature on animal signalling (for review see Espmark, Amundsen & Rosenqvist, 2000) may help clarify the evolutionary maintenance of altruism signals in humans by exploring the costs associated with encoding. This chapter has focused mostly on sender-dependent encoding costs (i.e. index signals), however there are multiple pathways to signal reliability that do not depend on sender-dependent costs (e.g. receivers may exploit or punish signalers – see Vehrencamp, 2000). If an altruistic character is detectable, then encoding costs and the sensory systems involved in decoding need more empirical elucidation.

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