SEXUAL SELECTION AND TRUST GAMES

Michael Stirrat

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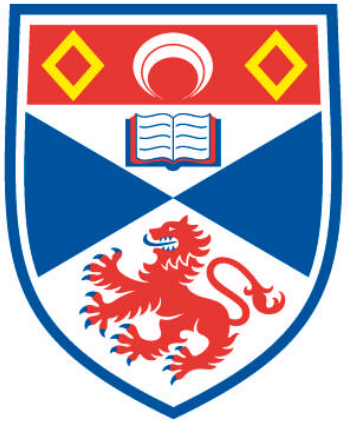

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SEXUAL SELECTION AND TRUST GAMES

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This thesis was submitted for the degree of Doctor of Philosophy in September 2009

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Note to the reader:

Throughout the experimental chapters in this thesis, I have used the pronoun ‘we’ instead of ‘I’. This work is my own in terms of hypotheses, analyses and conclusions, however, the Perception Lab is an inherently collaborative environment and all members assist in the running of participants, the taking of photographs, the setting up of software and experiments, the pooling of questions and data and the exchanging of ideas. Such collaborative effort must be acknowledged. The plural pronoun reflects the fact that, if published, the following experiments would carry multiple authorship and is used in keeping with intellectual honesty.

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"there is some particle of the dove kneaded into our frame, along with the elements of the serpent and the wolf." (Hume, 1898)

Abstract:

In economic games the facial attributes of counterparts bias decisions to trust and decisions to enter play. We report research supporting hypotheses that trust and reciprocation decisions in trust games are biased by mechanisms of sexual selection. Hypotheses that trust game behaviour is modulated by inter-sexual competition were supported. 1) Attractive individuals elicit more cooperation. 2) Male participants display trust and reciprocation toward attractive female counterparts in excess of perceived trustworthiness (and this display is modulated by male self-reported physical dominance). 3) Female participants appear to respond to male trust as a signal of sexual interest and are therefore more likely to exploit the trust of attractive males. 4) In explicitly dating contexts females are more likely to prefer attractive males to pay for the meal. These results indicate that participants are biased by mate choice and mating display considerations while playing economic games in the lab. Hypotheses that trust game behaviour is modulated by intra-sexual competition for resources were also somewhat supported. 1) Male participants reporting an ability to win fights with same-sex peers are more exploitative of other males. 2) Cues to current circulating testosterone level in counterpart's faces are less trusted but elicit more reciprocation. 3) The male sexually dimorphic trait facial width-to-height ratio (a trait which is related to both aggression and dominance) is related to an increased proportion of decisions to exploit others in the trust game while also being used by others as a cue to untrustworthiness. We conclude that trusting and trustworthy behaviour in both sexes is biased by mating market considerations predicted by intra- and inter-sexual selection

Section 1

Trustworthiness and Faces

Common sense tells us that we can judge the credibility and honesty of others from their demeanour and appearance. This is a view so commonly and clearly held that a study of Canadian court judges showed that they rely on common sense beliefs about the relationship between appearance, demeanour and credibility and may well have made incorrect court judgements upon this basis (Porte & ten Brinke, 2009). It is clearly important that we gain an understanding of how appearances bias decisions with regard to perceived trustworthiness. In this first section we will explore why humans are ever trustworthy, what information we can read from faces, and why attractive faces are trusted more.

Chapter 1. Trustworthiness has multiple evolutionary sources, one source is the cooperation required over reproduction leading to partner choosiness and costly signalling.

Chapter 2: Faces are rich sources of social information about personality and identity and as such may allow reliable and valid trust judgements.

Chapter 3: Attractiveness in the form of perceived health is trusted as a 'halo' but female attractiveness in the form of facial femininity elicits 'trust' unrelated to perceived trustworthiness. This may make sense in light of sexual selection for female fertility.

Chapter 1

Evolutionary Sources of Trustworthiness

It is easy to wax lyrical about trust and co-operation. Dawkins, that proponent of naked Darwinism and the 'selfish gene' does. He sees human society as "a delicate gossamer structure of trust and co-operation and, well, just plain niceness. Because I know and understand Darwinism, I see the threat lurking there just below the surface, ready to pull us down again." (quoted in Kohn, 2004, p. 323)

Without that "delicate gossamer structure" of trust social life would become a Hobbesian war of all against all; nature red in tooth and claw. Thomas Hobbes' solution to lack of trust was an authoritarian state with the sole legitimate use of force (Hobbes, 1651). This state would enforce social contracts and as a consequence trust would be underwritten because any defaulter upon legal agreement would have punishment meted out by the state. Hobbes' prescription of an absolute monarchy to solve the problem of cooperation and trust may not be a political pill that would be acceptable to swallow today but his writing on this point is perhaps the first statement of cooperation as a theoretical problem. It is because of this that it has tremendous value as a starting point.

Trust and cooperation and how they are implemented in social relationships or in the 'community' are regularly bruited by politicians. Lack of trust in politicians is a constant topic in the media and over many pints of beer the world over. Parents face very difficult choices of trust when they hand over their children at the school gate into the hands of people they hardly know. As consumers we place trust constantly in the standards of hygiene in restaurants, in the competence and motivation of the mechanics that repair our cars. Oddly, we are regularly willing to pay for services in advance trusting to receive services paid for; by doing this we wittingly give incentive

not to carry out the service we have already paid for and it is exactly this kind of incentive that Hobbes sought to counterbalance with government threat of force.

In popular media the books *The Selfish Gene* by Richard Dawkins (2006) and *The Origins of Virtue* by Matt Ridley (1996) cover most of the evolutionary bases of cooperative human nature. Given that the history of life is a history of natural selection, co-operation needs to be explained. Ridley notes that any animal behaviour is of necessity an evolved behaviour. The behaviour that exists is therefore most likely to be behaviour that has benefited its own replication. Rather than the behaviour benefiting itself, however, we should keep in mind an insight gained in evolutionary theory in making the distinction between replicators and vehicles (See Dawkins, 1982); any variation in behaviour between individuals (vehicles) that produces differential reproductive benefits for the source of that behaviour (replicators – e.g. genes) is behaviour that will be subject to selection (because the replicators will increase in number). To give an example, where there are genetic variations that produce differences in male mating displays, those genes that produce the most effective mating displays are the ones that will reproduce; it is the source of the behaviour that sees reproductive benefit. We should therefore always keep in mind when observing a cooperative behaviour the legal phrase *cui bono?* in English who or what benefits?

The common misunderstanding of Dawkins' metaphor of the *The Selfish Gene* (2006) is that this means the selfish individual. While Dawkins' metaphor may positively invite this misinterpretation this is clearly not what he means nor what would be predicted by evolutionary theory. Cooperative behaviours are predicted; their

original evolution can be explained by at least three evolutionary processes: (1) kin-selection (Hamilton, 1964), (2) direct reciprocity (Trivers, 1971) or indirect (Nowak & Sigmund, 2005), and (3) costly signalling (Grafen, 1990). All three of these mechanisms explain behaviour that looks costly for the individual by demonstrating how in the longer term the behaviour benefits the individual or their genes. We shall consider these three mechanisms but first we shall discuss how cooperation can be measured empirically.

Cooperation in economic games

Extensive research on co-operation has been carried out in the economic games framework. Classical game theory assumes the individual actor is *Homo economicus*; a perfectly rational, self-regarding actor whose only aim is to maximise payoffs. This individual will always be broadly self-interested and will maximise any payoff in an broadly defined economic context. This would not mean that individuals will never act to benefit others as there will be contexts of mutual self-interest as Robert Wright (2001) recently put it "among the many reasons I don't think we should bomb the Japanese is that they built my minivan." The source of co-operation in this framework is mutual self-interest, reciprocation.

The paradigmatic economic game is the Prisoner's Dilemma. The name of this game comes from the way it has been conceived and is normally introduced but the structure of the game appears in multiple co-operative and competitive contexts.

The Chicago District Attorney (DA) knows that two gangsters, let's call them A and B, are guilty of a serious crime but can only convict them if one or both of them

confesses. The DA picks them on a relatively minor charge and separately offers each of them a deal:

- If you confess and your accomplice does not, you go free (he goes to jail).
- If he confesses and you do not, you will get the maximum jail time (10 years).
- If you both confess, you will go to jail but the maximum sentence won't be applied (2 years).
- If neither of you confess, you will go to jail on a tax evasion charge – minimum jail time (0.5 years).

Players in this game get to choose how to treat the other guy, whether to rat on him (defect) or to keep their mouth zipped (cooperate). It will, however, always be self-interestedly rational to defect as can be seen from the years of jail time payoffs in Table 1-1. *Homo Economicus* would adopt a utility maximising strategy. With this assumption neither A nor B have any motivation to adopt the 'Don't confess' strategy. Consider B's options: if A chooses 'Don't confess' then B should choose to 'Confess' as this would reduce his six month sentence to zero, on the other hand if A chooses 'Confess' then it is still best for B to choose 'Don't confess' as two years is considerably less than 10. This situation is true for both A and B and they both also know that their counterpart will be able to reason the same way which provides even more motivation to switch strategies to avoid 10 years in prison.

John Maynard Smith (1982) has defined an evolutionary stable strategy (ESS) such as this one to be the best reply to itself that is a better reply to any alternative best reply than the alternative best reply is to itself. If this was easily understood we could dispense with the unpacking of the prisoner's dilemma above.

The upshot of this hyper-rational behaviour – finding the best reply to any other strategy – is that although the prisoners might co-operate to get only six months jail-

time they inevitably end up with two years each. The logic appears inescapable and suggests that organising co-operation and trust is impossible in this situation.

Table 1-1 - Prisoner's Dilemma Payoffs

		Prisoner A's strategies	
		Don't confess	Confess
Prisoner B's strategies	Don't confess	**(A)** 0.5 yrs **(B)** 0.5 yrs	**(A)** 0 yrs **(B)** 10 yrs
	Confess	**(A)** 10 yrs **(B)** 0 yrs	**(A)** 2 yrs **(B)** 2 yrs

In fact this logic is inescapable as long as the analytic assumptions hold that the players are consistent in behaviour, correctly understand the payoffs, and that the actual payoffs for the game are Prisoner's Dilemma payoffs. If the DA lies to the prisoners, some local mafia boss threatens the prisoners or the prisoners have a long term relationship of loyalty and reputation then the payoffs of the game are different from the payoffs of the Prisoner's Dilemma game. To put this more simply, the prisoners are not playing the Prisoner's Dilemma game and we should expect different behaviour. We must therefore be very careful in analysing game payoffs.

There is a similar game that can be used to measure trust and reciprocation rather than cooperation, this is the Trust Game. Originally popularised by Berg *et al* (1995) as the 'investment game' rather than making simultaneous moves as in the prisoner's dilemma, the second mover responds to the first mover.

The Trust Game is illustrated in Figure 1-1. In this version of the game all participants are given £3 at the start. Player 1 has a straight choice between whether to keep the £3 or entrust it over to player 2. An increment of £2 is applied to any entrusted money, increasing the total endowment to £8. Player 2 then has a choice to exploit

that trust and take an unfair proportion of the money (£6) or honour player 1's trust with a fair split of £4 each. As with the prisoner's dilemma, cooperation can benefit both players, in the Trust Game due to the increment, but player 2 can benefit more by defecting and taking an unfair share. Self-interest would therefore dictate that the player 2 would always cheat; due to this, rational self-interest would also dictate that player 1 should never trust.

The original version of the game allowed the first player to entrust the second player with any amount – including none – of the original endowment and the second player to return any amount of this final endowment. The binary version of the trust game we present here is simpler to interpret (Huck, Ruchala, & Tyran, 2007) as the choice is to trust or not to trust, to reciprocate or not to reciprocate and has been used and validated by various researchers as a measure of trust and reciprocity (c.f. Debruine, 2002; Fehr, Fischbacher, Schupp, Rosenbladt, & Wagner, 2003a; Glaeser, Laibson, Scheinkman, & Soutter, 2000; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005). This is the game that we have used to measure trust and reciprocity throughout the empirical reports that follow.

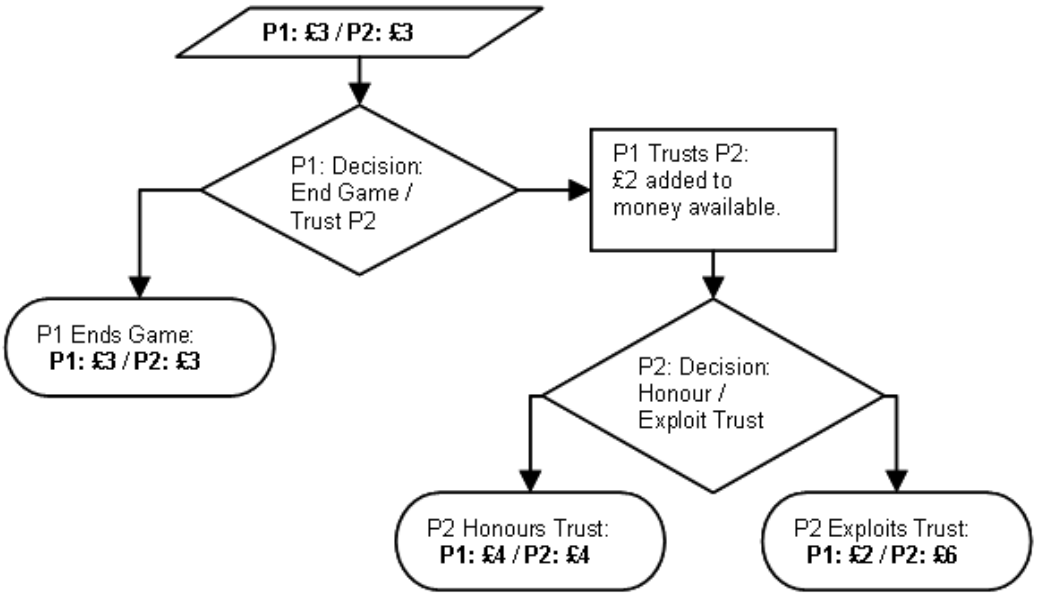

Figure 1-1 - Decision tree and payoff matrix for Trust Game: Player one (P1) has a binary choice between ending the game and trusting Player two (P2). P2 has a binary choice between honouring or exploiting trust. The monetary payoffs are explicit in the tree.

The typical behaviour of players in economic games including Prisoner's Dilemma and Trust Games is very far from the prediction of *Homo economicus.* Players choose to co-operate 50% of the time in Prisoner's Dilemma (Camerer, 2003), and if they get to communicate with their fellow 'prisoner' prior to the game this increases (Dawes, 1980). Participants in the various other experimental games show similar levels of co-operation and *non-rational* lack of self-interest. It is clear that either *Homo sapiens* is not also *Homo economicus* (See Henrich et al., 2004 for extended discussions) or players are playing different games from those set in the lab.

We can use this binary version of the Trust Game to illustrate one reason why predictions from the assumption of *Homo economicus* do not match with the way people actually play games. Whenever these games are played the assumption that the only payoffs are the monetary ones is not sustained. We can hold on to the assumption that players are self-interested when making decisions whether to be

trustworthy or not if we consider additional costs/benefits in the payoff matrix (Table 1-2) for being untrustworthy (Q) such as a feeling of anxiety at possible loss of reputation or pleasure at 'getting one over' on your acquaintance, and possible additional costs/benefits to being trustworthy (P) such as a 'warm glow' from feeling good about your actions or irritation at feeling taken advantage of. Also, when making decisions about whom to trust we may factor in other criteria (X and Y). We may trust others in order to convey respect, or honour, or that we like them in order to elicit some response; for example we might show trust to a problematic adolescent in order to provoke responsible behaviour even although we fully expect them to exploit our trust. On the other hand we may mistrust someone – or merely want to have nothing to do with them – in order to spite them rather than because we actually think they will exploit our trust. These additional factors (P, Q, X, and Y) are external to what happens in the lab and may explain some proportion of participant behaviour. With these additional payoffs the game participants are playing is not the Trust Game and we should therefore not be surprised when players are trusting or honour trust.

Table 1-2 – Trust Game payoff matrix. Player one (P1) has a binary choice between ending the game and trusting Player two (P2). P2 has a binary choice between honouring or exploiting trust. The monetary payoffs are explicit in the matrix but participants make decisions including extra payoff parameters, X and Y for trust decisions and P and Q for reciprocation decisions.

The Trust Game
Payoff Matrix

P1 / P2	Trust	Don't Trust
Honour Trust	£4+X / £4+P	£3+Y / £3
Exploit Trust	£2+X / £6+Q	£3+Y / £3

These other payoffs, however, require that participants believe that their actions will have consequences outside of the lab, i.e. we know our game counterparts or they know who we are. When these games are run it is therefore normal to control information completely so that participants are anonymous and are free to make choices without any social consequences but even then participants are honest and cooperative. A possible explanation why participants remain honest when unobserved is that they believe themselves to be observed. Indeed, priming participants with 'ghost stories' of a dead researcher who used to work in the lab and was interested in the outcome of experiments increased honesty in competitive lab experiments (Bering, McLeod, & Shackelford, 2006) or merely placing eyespots on the computer desktop background can increase cooperation in economic games (Haley & Fessler, 2005). Even placing a poster with eyes on it behind an honesty box increases the amount of money contributed (Bateson, Nettle, & Roberts, 2006). These studies indicate that even although all natural information is controlled, we still feel Big Brother watching us and behave to conserve our reputations. It has been suggested from facts like these that modelling fiction of *Homo economicus* might be abandoned in favour of the fiction of *Homo behavioralis* (Binmore, 1994). Where *Homo economicus* has preferences – albeit, evolved preferences – and decides how to act based upon those preferences the fiction of *Homo behavioralis* responds purely instinctively to stimuli and therefore behaviour is moulded directly by nature.

A more careful analysis of game payoffs is only one way of rehabilitating *Homo economicus*. People do not appear to behave in accord with the selfish rational actor model but the assumption of rationality can be moderated with what has come to be called *bounded rationality* (and see Gigerenzer & Selten, 2002; Simon, 1957, 1990);

this idea is that people are seldom aware of all the facts nor are they often able to deduce all the consequences and that it is these bounds on rationality that correctly explains the failure of individuals to behave in the fully rational expected manner. Under these assumptions the maximisation of utility is replaced with satisficing and the elegance and predictive power of game theory is retained. The position is well summarised by Kahneman (2003):

> "Economists often criticize psychological research for its propensity to generate lists of errors and biases, and for its failure to offer a coherent alternative to the rational-agent model. This complaint is only partly justified: psychological theories of intuitive thinking cannot match the elegance and precision of formal normative models of belief and choice, but this is just another way of saying that rational models are psychologically unrealistic."

An effect of this perspective is to push the level of decision making down from the individual's preferences toward adapted responses, either adapted in the weak sense of learned behaviour or in the strong sense of evolved psychological mechanisms (*Homo behavioralis*). The lack of realism present in *Homo economicus* may be due to the assumption that the source of cooperative behaviour is individual choice and that this choice is toward the end of benefiting the individual. *Bounded rationality* recognises that the source of behaviour may be elsewhere than individual choice.

Thinking about the evolution of the human species allows us to ask questions and hypothesise about both *Homo behavioralis* and the evolved preferences of *Homo economicus*. We shall, therefore, consider the sources of behaviour that underlie and bias cooperative decisions in the next section. It is however, worth noting here that heuristics of cooperative behaviour – unlike cooperation based on mutual self-interest – may in the end be indistinguishable from altruistic self-sacrifice.

Kin

First, a source of cooperation is kin selection (Hamilton, 1964). This is the reason that adults care for offspring, that ants sacrifice themselves for the colony and why as J.B.S. Haldane wryly observed: "I would lay down my life for two brothers or eight cousins." How does this work?

Animal behaviour has its source largely with the genes. Genes that predispose an animal to benefit its kin – those other animals that share the same genes – are genes that are likely to replicate more often than genes that don't do this. With other things being equal, parent animals that pay costs to benefit their offspring are more likely to reproduce and have offspring that reproduce than parent animals that do not do this. In the same way, but to a lesser degree, siblings that pay costs to benefit their sibs are more likely to have genes represented in the next generation. As Haldane observed, cousins are less related – the genetic relatedness of cousins being a quarter that of sibs – the same is true, more weakly, of behaviour toward cousins.

In the context of economic games and face perception there is evidence that we humans do exactly this in being more likely to cooperate with counterparts who look like kin in showing more trust to self-similar faces (Debruine, 2002) and contributing more in multiplayer economic games where some of the counterparts look self-similar (Krupp, Debruine, & Barclay, 2008).

Reciprocity

The prisoner's dilemma has a cooperative solution that relates to a second source of cooperation, reciprocity. As previously discussed the selfish rational utility maximising game player will always defect in the prisoner's dilemma. However, this is only the case if the player knows that this is the only game to be played, in the

jargon a one-shot game. If the game is iterated with the same counterpart the payoff structure over the longer term alters. The player may reason that it will benefit him to play nice and gain the benefits of cooperation with their counterpart for as long as the interaction continues. This is the logic of direct reciprocity (Trivers, 1971) and is nicely illustrated in Dostoyevsky's The Brothers Karamazov (Dostoyevsky, 1881), particularly in how the solution breaks down.

Dostoyevsky tells us of a Lieutenant Colonel responsibility for his division's accounts. The Lieutenant Colonel has struck up a relationship with a local businessman, Trifonov. Every month the Lieutenant Colonel closes the accounts, takes some money and loans it to Trifonov. Trifonov uses this capital to make a little profit and returns the money plus a little extra before the Lieutenant Colonel needs to write up the books for the next month. The Lieutenant Colonel trusts Trifonov to return the capital and Trifonov does so without fail. It quickly becomes apparent, however, that Trifonov is only trustworthy because he enjoys the benefits of the regular loans. The Lieutenant Colonel is suddenly posted and has to reclaim the outstanding capital quickly. Trifonov recognises that the relationship is at an end and responds with "I've never received any money from you, and couldn't possibly have received any."

When participants in the lab play iterated economic games the manner in which players start to stop cooperating is precisely in line with Trifonov's reaction and how close the participants recognise they are to the interaction ending (Dixit & Skeath, 2004; Roth, 1995).

There is a complication to this in our highly networked human interactions. Trifonov could only behave like he did because the relationship was somewhat clandestine. If

the financial relationship had been public and possible future financial partners would have access to information about Trifonov's behaviour he may have behaved quite differently. In any highly networked group we can expect that reputation will start to matter as counterparts may play with us according to how they have heard we played with someone else. This is indirect reciprocity (Nowak & Sigmund, 2005).

Again, reputation in economic games is important. When making economic game play decisions players are sensitive to information about how individuals have played previously (Huck, et al., 2007). Indeed, as previously mentioned, eyespots on the computer desktop background can increase cooperation in economic games (Haley & Fessler, 2005),

The idea of reputation leads on to the third evolutionary mechanism that may produce cooperation, costly signalling (Grafen, 1990).

Sexual selection

One area where cooperation, reciprocity or 'interchange' is absolutely required is in mating. Males and females must negotiate an interchange of sex gametes and care of offspring in such a way that the offspring come to term and survive to reproduce themselves. Individuals attempt to trade their various capacities of parental investment for other commodities and this leads to complex market problems of partner choice, advertising and the costs of recognising free riders.

Market effects influence the formation and development of mating relationships because there is intense competition over being chosen as a partner. The role of partner choice on the evolution of traits related to cooperation has been explained generally by biological market theory, demonstrating that partner choice can drive

organisms to adapt traits that that honestly signal an increase in their value as a cooperative partner (Noë & Hammerstein, 1994, 1995). In humans, males and females form long-term monogamous bonds and must select appropriate partners to develop such bonds with. Competition over partners in humans is strong, and therefore humans should be adapted to display traits that increase their ability to be chosen as a partner. Traits that could influence partner selection include access to resources, the disposition to provide resources and physical attractiveness (Buss, 2003).

There are sexual asymmetries to the reproductive costs of males and females, where the sex with the larger gametes (biologically defined as female) makes more physiological investment in their offspring. There is further asymmetry of investment in mammals since post-natally females provide nourishment to offspring through milk. This asymmetrical pattern of metabolic investment predicts that females will be choosier with partners and that males should seek as many mates as possible (Darwin, 1871; Kappeler & van Schaik, 2004; Trivers, 1972). This is because reproductive opportunity is physiologically cheaper for males than females. A male can inseminate numerous females with little physical cost, while a female can bear only single offspring at a time and incurs a large cost for each. Consequently, poor mate choices are more costly to a female's reproductive success, whereas males have much to gain and little to lose reproductively by obtaining many mating opportunities.

In humans, offspring also require extensive care before reaching sexual maturity, and so there is a very high demand on the female to care for her offspring. This

creates the need by the female to form a mate-bonded relationship with a male that can assist in providing resources and care to the infant. Consequently, females should have a selective bias towards males that can provide resources and support to her and her offspring, and this is provides a selective pressure towards monogamy (Kappeler & van Schaik, 2004). This generates a biological market based on sexual selection, where females prefer males that have traits that increase their ability to acquire resources and defend them. Consequently, when given a choice of different males, females will select the male that can best provide resources, creating a directional selective force towards traits related to resource holding potential. Males are forced to compete with other males by providing more and more resources in order to be chosen over other males by a female for a long-term mate. Here partner choice drives the evolution of the system. Since human offspring require high levels of care before reaching sexual maturity, males that can successfully provide the care and thus form long-term relationships with willing females will produce more viable offspring and will reproduce better than their other male competitors.

Sexual selection theory provides a framework for understanding the sex differences in human mate choice preferences. While men and women generally report the same desired characteristics in a long-term partner, they differ in what they consider to be most important (Buss, 1989). Men generally consider female attractiveness to be a necessity and resources to be a luxury whereas women more often consider male resources to be a necessity and male attractiveness to be a luxury (Li, Bailey, Kenrick, & Linsenmeier, 2002). Overall, human male courtship should involve the giving of resources, as signs of generosity, in order to out compete other potential mates of the female the male is courting (Miller, 2007). One example of such

advertising or ‘showing off’ among adult males is that men are more likely to make more generous donations to charity when observed by an attractive woman (Iredale, Van Vugt, & Dunbar, 2008). Males also show a disposition to provision females that are more likely to be sexually active and fertile. For example, males give greater amounts of money to females in the fertile phase of their menstrual cycle than to other females in lap-dancing establishments (Miller, Tybur, & Jordan, 2007).

If female choice between males, however, were simply a matter of choosing the male who showed greatest willingness and ability to invest in them and their offspring, this run-away selection pressure would produce resource-seeking males dedicated to provisioning females with necessary resources. Males who did not do this would not gain access to females, and would be out-competed and by their male rivals and would not reproduce. Males with the most resources may not have the most desirable traits in other characteristic though. Therefore, female choice should also attend to other cues that may indicate the male’s heritable qualities.

As we include other commodities into the market model, such as the need for additional resources to raise offspring successfully, trading becomes more complex and choices now become trade-offs. Females must decide how to trade-off between male dispositions to provide resources and other important fitness-related traits depending on their ability to acquire a mate. Females will select partners that can offer the best commodities depending on the choosing female’s relative value in the mating market. This market model generates the hypothesis that males with good genes (i.e., attractive males) will be required to provide fewer resources to gain sexual access, and attractive females will demand both attractiveness and additional

resources in a partner. Moreover, more attractive females should be more likely to test males for their ability to provide both genetic and economic benefits, by requesting resources from males they are attracted to.

A complication upon this mechanism is that individuals will evaluate their own mate value relative to others, in order to provide a subjective gauge of their ability to attract a romantic partner. A number of studies have shown that both self-perceived and other-rated attractiveness relate to one's ability to obtain romantic dates (De Vries, Swenson, & Walsh, 2008; Kurzban & Weeden, 2005; Walster, Aronson, Abrahams, & Rottman, 1966; Woll & Young, 1989). Self-perceived attractiveness should therefore relate to an individual's perception of their mate value. Since we expect market influences to play a factor in mate selection, one's assessment of their own value should be related to the qualities they demand from a partner (i.e., more attractive people will be more demanding of any prospective partner).

Attractiveness does seem to affect how one determines what qualities one seeks from a partner. For example, females with lower waist-to-hip ratios that scored low on measures of anxiety, depression and stress showed a higher preference for male physical indicators of male health (Jones, Little, et al., 2005). Females with lower waist-to-hip ratios and high scores for other measures of attractiveness showed preferences for more masculine male faces for long-term relationships (Penton-Voak et al., 2003). (We shall return to discuss masculinity as a marker for mate value in Chapter 2). Also, self-rated attractiveness in women has been shown to relate to preferences for facial masculinity and symmetry (i.e., attractiveness) in their partners(Little, Burt, Penton-Voak, & Perrett, 2001). Lastly, one study demonstrated

that female self-rated attractiveness was influenced by showing them images of either attractive or unattractive females (Little & Mannion, 2006). Females that observed images of attractive females downgraded their self-evaluation and those who observed unattractive images upgraded their self-evaluation. This effect shows clearly how the immediate market conditions might influence a female's perception of her mate value or competitive ability in a market of other females. This effect subsequently influenced female preferences for males in a manner showing that self-evaluation can influence their preference in a mating market. Females that were shown images of more attractive females showed lower preferences for male facial masculinity compared with females that were shown less attractive females.

There is little investigation on male self-perceived attractiveness but in one study, according to Little et al. (personal communication), males showed increased preference for female facial femininity if they consider themselves to be more attractive. It has also been argued that high-quality males are less likely to invest in mates and instead pursue a strategy of maximising their number of lifetime mates (Gangestad & Simpson, 2000). This is supported in that more physically attractive males are more likely to have more short-term sexual relationships than less attractive males (Rhodes, Simmons, & Peters, 2005). As with females, it seems the self-evaluation of males can influence how they select and invest in female partners in a mating market.

As a consequence of such trades, human romantic relationships seem to be influenced by the conditions of a mating market where partners are chosen based on

their quality as a partner relative to others in the market (Pawłowski & Dunbar, 1999).

In summary of this third mechanism leading to cooperation: Amongst sexual species there has to be some aspect of reciprocity in negotiating reproduction. On this basis further cooperation may evolve with parents cooperating extensively due to their mutual 'self-interest' in care of their offspring and partner choice. Where this is the case we should expect strong partner choice mechanisms (particularly in females) and costly signalling or 'advertising' of mate value (particularly in males). We should therefore expect such 'advertising' to consist in both display of resources but also display of generosity and willingness to share those resources (Iredale, et al., 2008; Miller, 2007; Miller, et al., 2007). We should also expect trade-offs to be made between cooperation and other resources all qualified against what competitors in the market offer.

These three processes demonstrably produce cooperative behaviour and are theoretically and empirically sound. Where manipulations under experimental conditions to ensure that human participants are not genetically related (excluding kin selection) preventing repayment (excluding reciprocity) and ensuring anonymity (excluding reputation formation or signalling) people still behave altruistically in economic games (e.g. Fehr & Fischbacher, 2003; Gintis, Bowles, Boyd, & Fehr, 2003; Henrich et al., 2005). This has been labelled 'Strong Reciprocity' and (mistakenly) been allied with Group Selection evolutionary arguments. Like our desire for sugar which is generally a good thing but is automatic and leads us to obesity, or our desire for sex being unrelated to whether we are using contraception or not, 'Strong

Reciprocity' in the laboratory is clearly maladaptive from a biological point of view as benefits cannot be accrued to any putative unit of selection, not the gene, not the individual and not any group (See Burnham & Johnson, 2005 for discussion). It is clear then that humanity has evolved heuristics of co-operation that are not introspectively aimed at kin or reputation. Trustworthy behaviour would seem, at least in part, automatic.

Here we have seen that there are sound evolutionary bases for trustworthy and cooperative behaviour. There are also, perhaps even more so, sound evolutionary bases for selfish behaviour and therefore if we can diagnose the sources of any given trusting or trustworthy behaviour we might understand better how it functions and encourage it in our lives or in society at large.

While it is true that any ultimate question of trust must start by looking at the origins of trustworthiness; in this thesis I do not wish to deal with the origins of trustworthiness generally. Nor do I wish to explore whether predispositions to be cooperative are innate, introspective and reciprocating or learned, social and categorical [there is evidence for this latter in internalised social norms (Gintis, et al., 2003) especially from children reporting that it is impossible to break social rules (Shtulman & Carey, 2007)].

The sources of human trustworthiness are various. Kin selective thinking has produced findings that human faces looking self-similar bias cooperative interactions as participants appear to favour those that look like kin (Debruine, 2002; Krupp, et al., 2008). Following a similar line my focus in this thesis has been on how aspects of

face perception, particularly attractiveness, in sexually selective contexts bias or alter trust and cooperative relationships.

The game theory fiction of *Homo economicus* has been used to predict cooperation between actors in many contexts ultimately based in mutual self-interest. It does not and can not predict all of the specific contexts where *Homo sapiens* will be biased. For that we need more biologically based thinking. Kin and sexual selection allow us to make predictions about human preferences but also to make predictions about automatic responses which may be unmediated by individual rationality. It is likely that humans respond to stimuli directly in ways that favour the replication of their genes without recourse to preferences.

First, we shall see how well we can read information about the predispositions of others from a very rich source of information, the face.

Chapter 2

Faces

Face reading has a very long history and has generated constant interest and controversy. The earliest mention of it appears to be in the book *Physiognomonica* which is commonly credited to Aristotle. Amongst many other bizarre ideas – at least to the modern reader – the writer of this book suggests that "large and outstanding ears" indicate a predisposition to "irrelevant talk," which is certainly a motivation to get those big ears pinned back as soon as possible if you want to be taken seriously.

More recently 'physnomye' was noted as an unlawful practice by statute of Henry VIII in 1530 and again banned in 1743 by George II (Stimson, 1910). This was done in the context of banning various practices, including palmistry, of the immigrant 'Egyptians.'

Assessment of character was again made popular in the 18th century by Johann Kaspar Lavater (1775-78) and although vigorously attacked by Hegel (1807) physiognomy remained a very influential idea, perhaps reaching it's modern height in Oscar Wilde's *The Picture of Dorian Grey* (1891) or in various short stories of Edgar Allen Poe (Grayson, 2005). This modern incarnation of physiognomy is also associated with Franz Joseph Gall through his popularisation of phrenology (Gall, 1796).

At various points in the 20th century the idea has been felt to be discredited. Francis Galton's early attempts to make composite faces of criminals found no discernible 'types' and in mainstream science, character has been assumed not to be readily discernible in appearances. But even so a survey of American university students in 1974 revealed that over 90 percent believed faces to be reliable guides to character and by 2000 this figure was not much less at over 75 percent (Hassin & Trope, 2000;

Liggett, 1974). Most likely as a result of this popular conception of the truth of appearances, the 1960 US election race between Nixon and Kennedy is generally reported as being swung in Kennedy's favour by a televised debate where Kennedy seemed healthy and relaxed and Nixon pale and sweating. It is a commonly repeated story that voters who had listened to the debate on radio thought Nixon had won, but that the television audience gave the win to Kennedy (Allen, 2007).

Such a clear general consensus on this matter that may even decide the outcome of US elections which are elections to governance of the biggest economic, military and political power there is, it is unarguably important that empirical work demonstrates what truth there is to physiognomy and how individuals are swayed by appearance.

Basic demographic information is clearly displayed in the human face. Human subjects are able to make very fast identification of the sex of faces with very high accuracy. This result has been replicated in a wide literature – as an example of this adult subjects presented with photographs of adults in which hair was concealed by a swimming cap performed with 96% accuracy (Burton, Bruce, & Dench, 1993). However, this skill must be learned as when presented with facial images masked to hide all hair and background information children aged less than 7 years performed at just better than chance, children aged around 9 were significantly less accurate compared with the near perfect accuracy in young adult subjects aged between 20 and 29 (Wild et al., 2000). A suggested reason for this is that children may change the way they represent faces from a piecemeal to a configural representation between ages 6 and 10 (Carey & Diamond, 1977).

There is much information about demography or identity in faces but there is also information about predispositions to behaviour.

Personality

The model of personality used by most researchers focused on the accuracy of social perception is the OCEAN or "Big Five" model of personality first proposed by (Norman, 1963) and subsequently extensively validated (McCrae & Costa, 1987). The five factors in this model have been given a variety of names but the OCEAN acronym is a contraction from openness, conscientiousness, extroversion, agreeableness and neuroticism. The earliest work using these factors in social perception demonstrated that after 15 minutes in the same room with a previously unknown individual and without verbal communication participants would rate their own extroversion, conscientiousness and openness with significant correlation to the other participants' ratings of them (Passini & Norman, 1966). These results have been replicated (e.g. Albright, Kenny, & Malloy, 1988; see Kenny, Albright, Malloy, & Kashy, 1994 for review) with extroversion and conscientiousness showing the most robust effects.

In all of the studies mentioned above participants made judgements using rich sources of information. Either the individual to be evaluated was present, behind a two-way mirror, or presented in high quality video. The effects remain even when the information available is reduced to facial information alone.

In a study using still facial images self-stranger ratings in extroversion, agreeableness and emotional stability (neuroticism) showed significant agreement. The 10 raters for each trait showed strong reliability for all personality traits with Cronbach's $\alpha>0.7$

on all parameters except male conscientiousness (α=0.625). For the male faces there was significant correlation between self and stranger ratings of extroversion, emotional stability and openness whereas only extroversion was significant for the female faces (Penton-Voak, Pound, Little, & Perrett, 2006). Although these effect sizes were small it remains that there was a significant relationship between personality variable perceived in the face and self-reported personality. In a second study, for each personality factor, the top and bottom 15 self-rated individuals were selected. Composite images were made of these to generate high and low factor images. These images were masked to hide hair, clothing and background. All the composites high in socially attractive personality characteristic (high openness, conscientiousness, extroversion, agreeableness and low neuroticism) were rated as more attractive but on controlling for attractiveness participants judgement were still accurate in assigning personality traits for both high and low agreeableness and high and low extraversion and additionally for the male faces between the high and low neuroticism composites.

Little and Perrett find very similar results also using composites of individuals who had rated themselves high or low on the OCEAN personality factors (Little & Perrett, 2007). The consensus for observer personality ratings between the 40 raters was also high with a Cronbach α>0.7 except for openness (α=0.56) and neuroticism (α=0.64). For female faces all factors except for openness showed significant accuracy in ratings between high and low factor composites. For the male faces only the high and low self-rated extroversion composites elicited significantly accurate ratings although all but agreeableness were in the same direction as the self-ratings.

Again, although the effect sizes were small these results demonstrate that some degree of personality is visible in the face.

However, this consensus about personality may be context-specific. The 'Big Five' personality model assumes cross-situational consistency; it is assumed that someone high in extroversion will be consistently high in extroversion throughout the majority of social contexts. Accuracy in evaluation of personality may well be spurious if any given individual's self report of personality is not consistent across contexts.

Indeed it has been argued that personality predicts very little of our behaviour compared with situation (Mischel & Shoda, 1995). However, agreement in personality judgements is not restricted to judgements of one's own group on the basis of local social norms, there is also cross-cultural consensus on perceived personality. American and Chinese participants agree upon perceived personality in both American and Chinese faces (Albright et al., 1997) although there are suggestions that the greater individualism of American culture allows greater consensus where the collectivised culture of Chinese participants encourages them to represent faces much more on the basis of social role, i.e. predicting behaviour from identity context rather than personality (Malloy, Albright, Diaz-Loving, Dong, & Lee, 2004).

In the competing predictions of situation dependent behaviour and personality dependent behaviour Buss (1989) argues that novel, formal and public situations, detailed instructions, little choice and brief duration favour an explanation of behaviour from the situation whereas the opposites of these favour a personality explanation (c.f. Chapter14, Eysenck, 1998, pp. 451-454 for discussion). Economic

games meet all the descriptive criteria for the former and from Buss's argument should be best explained by any individual's representation of the situation rather than conforming to any individual variation in innate predisposition or personality. A more complex picture is favoured by Atkinson *et al* (1993) who suggest that it would be more useful to interpret behaviour as being an interaction of personality and situation and put forward three forms of interaction: (a) reactive interaction: individuals interpret and experience situations in different ways, (b) evocative interaction: the behaviour of others is perhaps elicited by an individual's choice of behaviour toward them or (c) proactive interaction: individuals choose the situations they wish to enter.

Whatever the facts are, while personality may not predict all behaviour in any given situation, it does predict long-term predispositions and life behaviours and is significantly stable across contexts and time (McCrae & Costa, 1987).

This distinction, between individual differences and context specific determinants of behaviour is of crucial importance when not just evaluating personality or identity but when actually attempting to predict future behaviour of an individual from his or her appearance. We are able to do this somewhat with the OCEAN measures of personality but are we able to perceived honesty or trustworthiness in economic transactions from appearances.

Perceived Trustworthiness

One of the evolutionary sources of cooperation was reciprocity. Therefore when deciding about trust it would make sense to use faces to judge the likelihood of

cooperative behaviour in any given individual. How accurately can we evaluate trustworthiness from faces?

There is good reliability in ratings of honesty in faces. Zebrowitz *et al* (1996) report a Cronbach α=0.85 for ratings of facial photographs on a 7 point scale from *very deceitful* to *very straightforward*. The images presented were of people across a wide range of ages – from childhood through late 50s. Zebrowitz *et al* also report good reliability for ratings of attractiveness, babyfacedness, facial symmetry, eye size and expression positivity (an aggregate of two 7 point ratings from smile/no smile and happy/sad). All of these structural factors significantly predicted honesty ratings across most of the age range. This study also had access to clinical psychologists' previous assessment by interview with regard to honesty. This actual honesty measure was an aggregate of two Q-sort items: "is guileful and deceitful" and "appears straightforward, forthright, candid in dealing with others." There was no correlation found between clinician scores and rated facial honesty.

In contrast, and supporting the hypothesis that individuals can accurately detect honest disposition in faces Bond *et al* (1994) had North American students indicate how willing they were to sign up to run experiments involving deceit. The students were given descriptions of eight experiments which they could choose to participate in. Two of the experiments involved no deception but the other eight required the student to deceive participants – including offering non-existent rewards, pretending to be ill and making up answers to questions. Photographs were taken after the students had chosen which experiments they would be willing to be involved with. Ratings for facial honesty in these photographs significantly correlated with their

willingness to take part in the deceptive experiments. However Masip and Garrido (2001) failed to replicate the experiment with Spanish participants. They suggest that perhaps while North American facial stereotypes are accurate Southern European facial stereotypes are not. The only obvious difference in methods between this replication and the original experiment is that where Bond *et al* (1994) took photographs at the time of the experiment Masip and Garrido (2001) had students supply their own passport-type colour photographs at a later date. It is possible that as the photographs in this later study were likely not standardised (especially for interaction with the photographer) this noise masked personality information about the participants rendering later ratings inaccurate. It is also possible that as the images in the Bond *et al* (1994) study were taken directly after participants had decided whether to be deceitful the photographs captured information about level of arousal or current mood. If present, this information would allow subsequent raters to recognise the decisions that participants had made in that moment rather than long-term predispositions. In fact transient expressions can support accurate evaluation of non-cooperation, although static images taken before the experiment were not significantly correctly judged in an experiment by Verplaetse et al (2007) when participants rated the facial images taken of individuals at the time they were deciding whether to cheat participants were significantly accurate in identifying the cheaters. Perceptions of trustworthiness may relate to similarity to facial expressions such as anger or fear (Oosterhof & Todorov, 2009) but there is little evidence – apart from Bond *et al* (1994) – that biases based on stable facial traits are valid.

Participants watching videos of self-reported altruists rate them as more “helpful” than self-reported non-altruists; these self-reported altruists smile more (Brown,

Palameta, & Moore, 2003). Additionally, after a 30 minute interaction participants can predict the future behaviour of their partner in a Prisoner's Dilemma game (Frank, Gilovich, & Regan, 1993) although we are, in general, very bad at spotting when others lie (DePaulo, 1994; Ekman, O'Sullivan, & Frank, 1999).

Rather than being able to predict future behaviour in the form of predisposition to be dishonest Cosmides and Tooby (1992) have argued for a cheater detection module that recognises cheating and remembers who has honoured or violated social contracts in the past. Mealey *et al* (1996) lend this idea some support. Participants were shown faces accompanied by a blurb indicating that the person in the photograph has either a history of cheating, irrelevant information, or a history of trustworthiness. A week later the participants were called back and were asked to rate the same photographs and also indicate which they remembered as having seen the previous week. The participants showed a significantly better memory for the faces labelled as having a history of cheating. However, Barclay and Lalumiere (2006) suspected that there was asymmetry in the descriptors of cheaters and cooperators such that while cheaters were associated with a strongly emotive blurb the cooperators were not. They attempted to replicate the study but excluded both descriptions of cheaters and cooperators that were not cleanly categorised. They excluded descriptions of cheaters from Mealey *et al* (1996) that were also threatening or physically dangerous. They also excluded descriptions of cooperators that were altruistic or socially threatening rather than cleanly trustworthy. After controlling for this asymmetry they found no enhanced memory for any group.

Consistent with Mealey *et al* (1996), and without using descriptions, Yamagishi *et al* (2003) found that participants had a better memory for faces of individuals who were photographed at the moment they defected in a Prisoner's Dilemma game. They also found that participants were more likely to report they falsely recognised defectors than co-operators. This suggests a systematic difference in the facial information present in co-operators and defectors – although Yamagishi *et al* (2003) report that participants do no better than chance when asked to identify which faces are those of co-operators and which of defectors.

Rather than having an ability to recognise untrustworthy individuals, we recognise when people are being untrustworthy and remember them.

We may also have mechanism to adapt to local contexts and trust according to associations with familiarity. Buckingham et al (2006) find that participants adapt to faces they are presented. Participants were shown a slide show of 15 male faces and asked to memorise them. These faces were manipulated to be either more masculine or more feminine. Participants then made forced choices between two faces also manipulated for sexual dimorphism as to which looked more trustworthy. The exposure to masculine or feminine male faces increased subsequent attributions of trustworthiness to the type seen.

This may relate to other reasons for 'trusting' previously discussed such as kin selective sources of cooperation. In testing whether kin selection may be implicated in decisions about facial trustworthiness DeBruine (2002) manipulated same-sex facial images to look either more self-similar or more similar to another unknown participant. Lending some support to the idea of kin selection in this instance,

trusting behaviour was indeed increased toward the self-similar faces and unaffected in the control condition. The level of reciprocity was not different when trusted by a self-similar counterpart versus an other-similar counterpart.

It is possible that this result could be driven by self-similar facial images being considered more attractive. DeBruine (2005) follows this possibility up by testing self-similar opposite-sex facial images for trustworthiness, attractiveness for a long-term relationship and attractiveness for a short-term relationship. The same-sex results of the previous work are replicated with opposite-sex faces; the self-similar opposite-sex faces in this study are more trusted than other-similar faces. The attractiveness judgements differ from this; opposite-sex self-similar faces are judged to be less attractive for a short term relationship and no different from stranger-similar faces for attractiveness for a long-term relationship. This demonstrates that there is something like a kin selective preference for trusting self-similar faces that is not simply due to attractiveness.

But why would we think that attractiveness would bias decisions about trustworthiness anyway? The evidence is that attractiveness predicts ratings of facial honesty. Attractiveness also predicts trust behaviour in games of strategy. Participants in a study by Mulford *et al* (1998) are both more willing to play games of strategy with and once playing, more likely to cooperate with more attractive participants in prisoner's dilemma games apparently because participants expect attractive counterparts to be more cooperative. In Mulford *et al* (1998) this expectation is to some extent borne out, the attractive male individuals are more likely to be co-operative although attractive females are not. This suggests that

evaluations of trustworthiness – at least with males – are not merely ecologically valid, i.e. reliably made, but may also be functionally valid, i.e. have the intended consequences. Participants also offer attractive participants greater rewards (but demand more from them as well) in ultimatum games (Solnick & Schweitzer, 1999). And in trust games (Wilson & Eckel, 2006).

In other studies, however, attractive individuals have not been found to be more cooperative (Zebrowitz, et al., 1996) or have been found to be systematically less cooperative (Takahashi, Yamagishi, Tanida, Kiyonari, & Kanazawa, 2006; Zaatari & Trivers, 2007).

We shall come back to attractiveness and the reasons it biases trust decisions in future chapters – but to tip my hand, think sexual selection. While males prioritise female attractiveness in mate choices, as discussed in the previous chapter females are likely to prioritise resources and investment behaviour. What is considered 'attractive' in a mate will be different between the sexes, and how individuals compete with their own sex is likely to differ between the sexes as well.

Signals of masculinity in males may indicate resource holding potential. Secondary sexual characteristics such as male facial masculinity are related to testosterone. Specifically, testosterone increase in response to winning competitive games is such that facially masculine men have a greater response (producing more circulating testosterone) than do other men as a result of winning a competitive task (Pound, Penton-Voak, & Surridge, 2009).

One explanation why greater expression of testosterone as facial masculinity might be attractive is that it may cue immunocompetence, possibly because testosterone

stresses the immune system, so that only healthy males can afford large male traits (Folstad & Karter, 1992; Thornhill & Gangestad, 1999). Other explanations why masculinity should be attractive are that it may cue higher status or greater dominance (Buss, 1989) or that facial masculinity is related to measures of symmetry, specifically fluctuating asymmetry (FA) such that masculine males are more symmetric (Gangestad & Thornhill, 2003) and low FA is attractive (Perrett, 1999). This FA in men is in turn associated with reduced cooperation in economic games (Zaatari & Trivers, 2007). Therefore amongst other things, masculinity and the hormone testosterone are likely to be relevant to cooperation, face perception and female mate choice because male dominance or heritable health should be attractive to females.

Level of testosterone predicts economic game behaviour. Males with higher circulating testosterone are more likely to punish unfair economic game offers (reactive aggression) than are individuals with lower circulating testosterone (Burnham, 2003). High testosterone in men is also associated with increased aggression and behaviours aimed at achieving or maintaining high status (Archer, 1991; Mazur & Booth, 1998; Olweus, Mattson, Schalling, & Low, 1980; Zitzmann & Nieschlag, 2001).

Evidently the relationship between masculinity and male attractiveness is complex because cues to dominance and heritable health may also cue somewhat anti-social behaviour and while male attractiveness is clearly related to health and dominance it is also related to being prosocial (Farrelly, Lazarus, & Roberts, 2007; Hardy & Van Vugt, 2006; Jensen-Campbell, Graziano, & West, 1995; Roney, Hanson, Durante, &

Maestripieri, 2006). There should therefore be tradeoffs in female choice between cues to status, heritable health benefits and predispositions to less pro-social behaviour (see Rhodes, 2006 for discussion).

Women do indeed appear to make tradeoffs in what they see as attractive. During the menstrual cycle phase of highest conception risk female participants show increased preference for deeper (more masculine) voices (Feinberg, 2006), for the odour of more dominant males (Havlicek, Roberts, & Flegr, 2005), for masculine faces (Johnston, Habel, Franklin, Fink, & Grammer, 2001; Penton-Voak et al., 1999), and reduced attention to perceived health (Jones, Perrett, et al., 2005). In a review of this literature Jones *et al* (2008) conclude that preferences for apparent health and self-resemblance are aimed at increasing the probability of successful pregnancy by avoiding contagion and improving social status whereas the evidence for masculinity preferences is equivocal between this and possible heritable benefits.

Testosterone appears to be an explanatory factor for masculine traits and is also a component determining face preferences within individuals. Welling *et al* (2007) demonstrated that when making attractiveness judgements for male faces across the female cycle, females show an increase in preference for masculine male faces over feminine male faces when circulating testosterone is higher than at other points in the cycle (and other hormones are constant). A preference for more masculinity in males would be consonant with increased risk-taking and a reduced restriction in attitude to casual sex.

Physiological effects of testosterone could to some extent explain more masculine behaviours in women. Schreiner-Engel *et al*. (1981) found positive correlations

between female salivary testosterone levels and genital response to erotic stimuli in the laboratory. Tuiten *et al* (1996) confirm testosterone as a mechanism for this, rather than a correlate, when they found that genital response was increased in amenorrheic women by testosterone administration. The North American Menopause Society (2005) has also found positive enhancement of sexual function in menopausal women with regard to desire, arousal, and orgasm with application of topical testosterone over that driven by placebo.

Raised testosterone in women does not only increase male-typical attitudes in women with regard to sex. Dabbs *et al* (2002) show that participants of both sexes describe feelings of increased arousal and, noteworthy here, aggression. Participants scored more highly on implicit-attitude measures of arousal and aggression when their testosterone level is increased by application of testosterone gels to the skin when compared with a placebo. The placebo condition also showed significantly greater self-report and implicit measures of arousal and aggression than participants who ingested liquorice capsules (which lowers testosterone). The effects were stronger for women that for men. This supports the idea that just as high average basal testosterone males tend to be aggressive (Archer, 1991) high testosterone females are likely to be similarly aggressive and dominance seeking.

These reported effects of testosterone upon female physiology and behaviour support the contention that testosterone has similar effects upon females and males. It is therefore likely, although not demonstrated, that naturally occurring variation in testosterone amongst women may also affect female facial appearance in a way that allows prediction of behaviour. Given that male testosterone measures

predict ultimatum game punishment for unfair behaviour (Burnham, 2003) it is likely that female circulating testosterone measures and facial correlates would also predict punishment.

Why Trust Attractive People?

We have evolved or learn capacities to read the predispositions of others in personality or current emotional state (or relatedness). We are likely to preferentially trust others whose facial features relate to reduced costs or increased benefits in some systematic manner. For example, if someone looks like kin, it may be likely that they are kin and therefore in the long term, acting to help those that look like kin has increased the replication of those genes that specify this behaviour.

In the next chapter we discuss what is trusted about attractive faces.

Chapter 3

Attractiveness and Trust

Abstract: Choices about entering affiliative relationships are influenced by attractiveness. Our aim here was to determine facial cues relevant to attractiveness that influence trust decisions. In two experiments participants decided whether or not to trust faces of peers presented in neutral pose. We tested for associations between trust and facial attributions of health, attractiveness, masculinity and age. In experiment 1 perceived health explained the largest proportion of the variance in trust for both sexes but with facial masculinity and attractiveness also predicting trust placed in male faces. In experiment 2 we distinguished between perceived trustworthiness and trust decisions. We found that perceived trustworthiness was the strongest predictor of trust decisions and that only female sexual dimorphism independently contributed to these decisions (perceived health did not). When we considered which factors predicted perceived trustworthiness we found that perceived health and female age were the strongest predictors. We conclude that perceived health is a major factor in driving judgements of trustworthiness. This may be because association with healthy individuals increases the likelihood of durable future support and reciprocity. We also noted that whereas attractiveness (particularly in the form of perceived health) contributes to perceived trustworthiness in both sexes female attractiveness (in the form of femininity) creates a 'beauty premium' which elicits 'trust' decisions in excess of perceived trustworthiness.

In an elegant series of Trust Games Wilson and Eckel (2006) clearly demonstrated that the attractiveness of others influences our decisions whether to trust them. We place more trust in attractive than unattractive individuals; in Wilson and Eckel's terminology we pay a "beauty premium" when we decide to trust.

Why did participants place more trust in attractive counterparts? First, it is consistent with much other literature that shows that there is a 'halo' around attractive people. We have stereotypes about attractive people and assume them to be intelligent, competent, successful, and all-round better people (Langlois et al., 2000); and we may even pay them more for doing the same jobs (Bull & Rumsey, 1988). We may simply trust attractive people because we believe them to be more trustworthy and therefore assume that we will gain from trusting them. It was certainly true in Wilson and Eckel's study that more attractive individuals were rated as more trustworthy and were more trusted in the games.

Second, Wilson and Eckel note that there may be evolutionary reasons for behaving positively towards attractive people, as their attractiveness may cue 1) 'good genes', 2) good parental investment or 3) high social status. We may want to buy into being their social affiliates for any of these reasons even if we do not actually feel trust for them more than others. Participants in Wilson and Eckel's trust games may have trusted others in order to gain payoffs external to the game (X or Y in Table 1-2); participants might gain social status or affiliates by trusting. This does not require that individuals consciously evaluate their counterparts; the fact that these type of experiments are conducted between strangers with a very low probability of individuals ever interacting again but still produce these results suggests that

conscious evaluation of this kind is not a motivator. Instead we may have evolved a predisposition or learned a heuristic to behave well toward those in society we can benefit from as friends or as mates.

The way the explanations from an attractiveness 'halo' or from evolved predisposition differ is exactly in where the benefit to individuals is in the payoff matrix (Table 1-2). If we trust attractive people because we believe them to be more trustworthy then the payoff is monetary whereas if we behave like this because we desire to affiliate ourselves with the individual to gain social status or 'good genes' then the payoff is external to the game i.e. in X or Y.

As already stated, the results of Wilson and Eckel's experiments showed that to some extent the payoff may have been monetary. Participants reported that they expected the attractive people to reciprocate their trust more than the less attractive people. In support of this interpretation, when trusted, counterparts in the 'unattractive' group of Wilson and Eckel's study were actually less trustworthy (returned less cash on average than they had been entrusted with) than the 'attractive' groups of counterparts (who on average returned more than they were entrusted with).

It is interesting to note that while attractive people are more often trusted in these games this did not necessarily mean that the attractive participants earned more. Participants also applied a "beauty penalty." When trusted by an attractive compared with an unattractive counterpart participants returned more to the unattractive counterparts. This effect seems to have been driven by greater expectations of positive behaviour from the attractive trusters. Wilson and Eckel

asked how much they thought their counterpart would entrust to them. When the actual amount was higher than this expectation the attractiveness of their counterparts made no difference in the amount participants returned; when the amount entrusted was lower than expected participants returned significantly less to attractive than unattractive counterparts.

It appears from this then that attractiveness elicits more trust (and attractive people are more trustworthy) but also that we expect more of attractive people and punish them more severely when they default on these expectations.

The experiment reported here attempts to replicate and extend Wilson and Eckel's experiment. Faces that are considered to be more attractive may be so for various reasons. Ratings of facial attractiveness are related to perceived health (Rhodes et al., 2007), sexual dimorphism (Perrett et al., 1998), symmetry and averageness (see Rhodes, 2006 for review). Symmetric faces are attractive because they have a healthy appearance (Jones et al., 2001). Immune system health in the form of MHC-heterozygosity has been demonstrated to relate to attractiveness judgements (Roberts, Little, Gosling, Perrett, et al., 2005) and MHC dissimilarity also predicts attractiveness judgements (Roberts, Little, Gosling, Jones, et al., 2005). Youth is also related to female attractive alongside sexual dimorphism (Barber, 1995).

These factors: perceived health, age, and sexual dimorphism should drive attractiveness judgements. We therefore conducted two experiments. In the first experiment participants played trust games while observing their counterpart's facial image. These images were previously rated on attractiveness, health, youth and sexual dimorphism. The second experiment was conducted similarly but in order to

distinguish perceived trustworthiness from trust decisions the facial images were rated for perceived trustworthiness.

Experiment 1 – Perceived Health and Trust

Images

We began with a collection of 132 white face images (66 male; mean age 20.5 years, SD = 2.25). Nineteen participants (white and aged 18–24) rated the images on various parameters. Images were masked (to exclude hair and clothing) and presented in random order. Each image was assessed on a likert-type scales of 1–7 for (i) attractiveness; (ii) health, (iii) masculinity of male faces, (iv) femininity of female faces and finally (v) an estimation of age.

Participants

50 female and 58 male white students (age 18-24) at St Andrews University were recruited to take part in the trust games.

Procedure

Participants took part in a sequential trust game as defined in Chapter 1. Past experience of behaviour influences trust judgements (Paunonen, 2006) therefore in order to explore the bias of facial appearance participants must play the trust game with unfamiliar (zero-acquaintance) partners.

Participants were given written instructions on how the game was played (see Appendix 1) and a flow chart of the game was present on screen throughout (See Appendix 2). Masked images (to exclude hair and clothing) were presented in random order and participants played as player 1 in all games. The only information available to them about player 2 was the presented image.

Participants had their photograph taken and were told that once they decided how to play in any given game the outcome of games would be dependent on the previous behaviour of their counterpart. Outcomes were randomly generated biased by the actual previous behaviour of participants (i.e. a counterpart that had previously reciprocated 90% of games would randomly reciprocate 90% of games).

Participants took part for course credit and played the game with virtual money.

Results

As ratings of faces may tap into similar structures multi-collinearity might have been a problem for any or all of these analyses. We therefore checked at each level of analysis but none of the analyses reported a VIF value greater than 7.8 and most were considerably less than this.

The facial attractiveness of counterparts correlates with how participants place their trust. All rated parameters of the 132 images correlated with the proportion of participants trust placed in them (Figure 3.1). Linear regression predicting trust of image with other-rated age, attractiveness, health, and sexual dimorphism explained ~38% of the variance with (all VIF < 3.37). In a comparable stepwise regression analysis we found that health alone explained ~33% of the variance ($r^2 = 0.334$, beta = 0.57; $p < 0.0005$ – see Figure 3.1) and there was no independent contribution from any other parameter.

Images were split by sex and the data reanalysed.

132 images (66 male / 66 female)	% Participants Trusted	
Health	R = 0.58,	p < 0.0005
Age	R = -0.19,	p = 0.032
Sexual Dimorphism	R = 0.19,	p = 0.028
Attractiveness	R = 0.53,	p < 0.0005

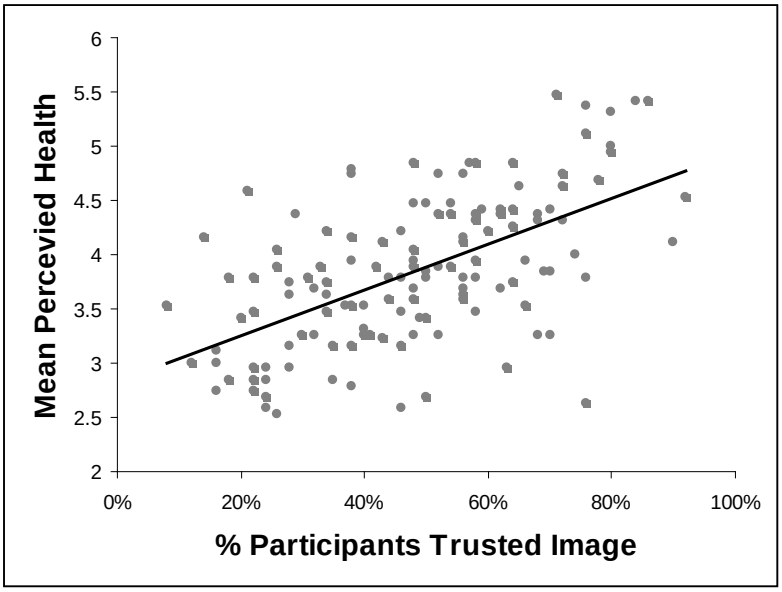

Figure 3-1 – All rated parameters correlated with trust decisions.
Perceived health showed only independent contribution to regression model.

Female images

With the 66 female images there were significant correlations between trust and ratings of attractiveness ($r = 0.56$ $p < 0.0005$), perceived health ($r = 0.62$ $p < 0.0005$), femininity ($r = 0.58$ $p < 0.0005$) and perceived age ($r = -0.27$ $p = 0.03$). Linear regression predicting trust of image with other-rated age, attractiveness, health, and sexual dimorphism explained ~40% of the variance with (all VIF < 7.8). In a comparable stepwise regression model of trust decisions only perceived health was a significant predictor ($r^2 = 0.38$; beta = 0.62; $p < 0.0005$).

Male images

With the 66 male images there were significant correlations between trust and ratings of attractiveness ($r = 0.52$ $p < 0.0005$) and perceived health ($r = 0.56$ $p < 0.0005$). No effects were found for perceived age ($p = 0.35$) and masculinity ($p = 0.13$). Linear regression predicting trust of image with other-rated age,

attractiveness, health, and sexual dimorphism explained ~43% of the variance with (all VIF < 3.1). In a comparable stepwise regression model of trust decisions perceived health, masculinity and attractiveness were all significant predictors (r^2 = 0.42; perceived health beta = 0.3, masculinity beta = -0.33, attractiveness beta = 0.36; $p < 0.0005$).

Experiment 2 – Perceived Trustworthiness and Trust

In order to distinguish between perceived trustworthiness and trust decisions made for other reasons we ran a second study with images previously rated for perceived trustworthiness. We were also concerned that games played without real monetary payoffs may be played solely according to perceived trustworthiness rather than with any real-world pay-off in view. Participants therefore received real monetary payoffs.

Images

We selected 99 white face images (49 male; age 18-25). Nineteen participants rated the images on various parameters. Images were masked (to exclude hair and clothing) and presented in random order. Participants were white and aged 18–24. Each image was assessed on a likert-type scales of 1–7 for (i) attractiveness; (ii) health, (iii) masculinity of male faces, (iv) femininity of female faces, (v) an estimation of age, and (vi) an estimation of how trustworthy the individual looked.

Participants

49 female and 14 male Caucasian students (age 20-23) at St Andrews University were recruited to take part in trust games.

Procedure

Participants took part in a 'two-person' sequential trust game as defined in Chapter 1 with unfamiliar (zero-acquaintance) partners.

Participants were given written instructions on how the game was played (see Appendix 1) and a flow chart of the game was present on screen throughout (See Appendix 2). Masked images (to exclude hair and clothing) were presented in random order and the participants were randomly assigned as player 1 or 2 for each game (seeing each identity of image in only one game). The only information available to them about their counterpart for each game was the presented image.

Participants had their photograph taken and were told that once they decided how to play in any given game the outcome of games would be dependent on the previous behaviour of their counterpart. Outcomes were randomly generated biased by the actual previous behaviour of participants (i.e. a counterpart that had previously reciprocated 90% of games would randomly reciprocate 90% of games). Participants were informed that the game outcomes would be paid in cash and converted at a lab exchange rate that would mean that final payment would be equivalent to the outcome of one game.

Results

Trust (player 1) and reciprocation (player 2) decisions correlated with all image ratings (see Table 3-1). Linear regression predicting trust of image with all image ratings explained ~74% of the variance with (all VIF < 5.9). In a comparable stepwise regression only perceived trustworthiness and sexual dimorphism predicted trust decisions ($r^2 = 0.74$; trustworthiness beta = 0.26, sexual dimorphism beta = 0.03; p <

0.0005; VIF = 1.22). In a t-test participants did not show significantly different amount of trust in this experiment compared with experiment 1 (p = .72).

Decisions to reciprocate trust also correlated with all image ratings (see Table 3-1). Linear regression predicting trust of image with all image ratings explained ~33% of the variance with (all VIF < 5.97). In a comparable stepwise regression perceived trustworthiness was also the best predictor for this but perceived health and age also explained some of the variance (r^2 = 0.33; trustworthiness beta = 0.05, perceived health beta = 0.04, perceived age beta = -0.013; p < 0.0005; VIF < 1.82).

A stepwise regression predicting perceived trustworthiness from perceived health, age, sexual dimorphism and attractiveness found that only perceived health and age were independent predictors (r^2 = 0.45; perceived health beta = 0.445, perceived age beta = -0.079; p < 0.0005; VIF = 1.004).

Table 3-1 – Perceived ratings correlate with trust and reciprocation decisions.

99 images (49 male / 50 female)	% Participants Trusted	% Participants Reciprocated
Perceived Trustworthiness	r = 0.85, p < 0.0005	r = 0.51, p < 0.0005
Perceived Health	r = 0.59, p < 0.0005	r = 0.48, p < 0.0005
Perceived Age	r = -0.22, p = 0.028	r = -0.27, p = 0.008
Perceived Sexual Dimorphism	r = 0.47, p < 0.0005	r = 0.34, p = 0.001
Perceived Attractiveness	r = 0.62, p < 0.0005	r = 0.46, p < 0.0005

Data was split by sex of image and data reanalysed.

Female images

Stepwise regression showed perceived trustworthiness and femininity to be independent predictors of trust decisions (r^2 = 0.80; trustworthiness beta = 0.28, femininity beta = 0.05; p < 0.0005; VIF = 1.79).

Decisions to reciprocate trust with female images was predicted by both perceived trustworthiness and health (r^2 = 0.72; trustworthiness beta = 0.11, perceived health beta = 0.07; p < 0.0005; VIF = 2.09). Excluding perceived trustworthiness from the

analysis allowed a significant model (r^2 = 0.61; perceived health beta = 0.12; p < 0.0005).

A stepwise regression predicting perceived trustworthiness from perceived health, age, sexual dimorphism and attractiveness found that only perceived health and age were independent predictors (r^2 = 0.76; perceived health beta = 0.434, perceived age beta = -0.093; p < 0.0005; VIF = 1.12).

Male images

Stepwise regression showed perceived trustworthiness is a significant predictor of trust decisions (r^2 = 0.70; trustworthiness beta = 0.25; p < 0.0005). No other image rating independently contributed to the model.

Decisions to reciprocate trust with male images were not predicted by any other rated facial parameter (all p > 0.6).

A stepwise regression predicting perceived trustworthiness from perceived health, age, sexual dimorphism and attractiveness found that only perceived health was an independent predictor (r^2 = 0.62; perceived health beta = 0.448; p < 0.0005).

Discussion

In line with the results from Wilson and Eckel (2006) we find a strong relationship between attractiveness and trust. We did, however, find that perceived health was a stronger predictor of perceived trustworthiness with perhaps an independent contribution from female youth and male masculinity and attractiveness.

There was no significant different in the proportion of trust decisions between the unpaid condition in experiment 1 and the paid condition in experiment 2. In experiment 1 where participants were unpaid we found that perceived health (and

male masculinity and attractiveness) predicted decisions to trust counterparts. In experiment 2 we found that perceived health (and female youth) predicted rated trustworthiness.

In experiment 2 we found that perceived trustworthiness was the most significant predictive variable in regression models of actual trust game decisions played with real monetary payoffs. The only other perceived facial attributes that independently predicted trust decisions was female femininity. This is noteworthy as it is a first step toward teasing apart which facial attributes may drive perceived trustworthiness and which may drive what Wilson and Eckel called a 'beauty premium.'

Participants in our games trusted healthy people. This may be because healthier individuals are more trustworthy. Health is predictive of altruism in the second player role of trust games (Fehr, Fischbacher, Schupp, Rosenbladt, & Wagner, 2003b). Indeed there is more general evidence that healthy individuals are those that are volunteers, giving to others appears to enhance one's own health (Brown, Consedine, & Magai, 2005) and therefore perceived health may be a good proxy for trustworthiness. Or perhaps health is related to a disposition to positive affect and therefore salient (particularly in men) as an attractive and prosocial feature (Jensen-Campbell, et al., 1995; Roney, et al., 2006) particularly as prosociality leads to high status (Hardy & Van Vugt, 2006) and altruism is attractive in and of itself (Farrelly, et al., 2007).

The evidence here suggests that facial attributes affect trust decisions in two ways. Trust is placed in healthy individuals (as well as in less masculine men and youthful women) because participants perceive them to be trustworthy whereas facial

femininity in women elicits 'trust' in excess of perceived trustworthiness. Whereas trusting those we perceive as trustworthy could reasonable be seen as aimed at gaining the extra payoff in the Trust Game, trusting a counterpart in excess of how trustworthy they appear to be would seem to be aimed at gaining payoffs external to the Trust Game (X or Y payoffs in Table 1-2).

Perceived Health is Trusted, Femininity is 'Trusted'

Our data is in line with Wilson and Eckel's findings that attractiveness is both used as a cue to trustworthiness and as something more, in their words a 'beauty premium.' From our data, perceived health appears to be the component of attractiveness that is the most significant driver of perceived trustworthiness and female facial femininity emerges as the only component of attractiveness measured that elicits the excess 'trust' of a 'beauty premium.'

Wilson and Eckel did not find any effects from participant sex other than that females returned more when trusted by male participants. While Wilson and Eckel (and also Andreoni & Petrie, 2008) found effects of attractiveness and no effects of sex on game play they did not test for interactions between sex of participants and differential effects of opposite sex attractiveness. This may not matter if attractiveness cues social status but if attractiveness cues 'good genes' or parental investment then we should expect that female attractiveness and male attractiveness have differing effects upon male and female observers. With this in mind, femininity does not have a clear relationship with health but may rather be related to fertility (Johnston, 2000; Johnston & Franklin, 1993; Rhodes, 2006; Symons, 1979). Indeed facial femininity has been shown to positively associated with oestrogen, an index of reproductive health (Law Smith et al., 2006). We would

therefore expect that female facial femininity should be attractive to males when making mate choices as over evolutionary time males' attraction to fertile and fecund females would likely have been selected for.

We did not split these studies by the sex of participants as the experiment had not been designed with this in mind but we should expect that males – but not females – should be affected by female facial femininity as a mate choice relevant attribute and therefore that males – but not females – should be placing excess 'trust' in attractive female counterparts.

This anaysis, that facial features relevant to mate choice are implicated in Trust Game decisions, suggests that behaviour in economic games is susceptible to bias from psychological mechanisms that have little to do with *Homo economicus* preferences and everything to do with instinctive response to the imperative to reproduce.

In the next few chapters we will explore possible sexually selective effects influencing participant play in the trust game.

Section 1 Summary:

Trustworthiness has multiple evolutionary sources, one source is the cooperation required over reproduction which leads to partner choice and costly signalling. Faces are a rich information source of personality and social identity and as such may allow reliable and valid trust judgements. Facial attractiveness is seen as trustworthy, as a 'halo' and this aspect of facial attractiveness is somewhat based in perceived health. Female attractiveness related to femininity elicits excess 'trust' that is unrelated to perceived trustworthiness. This may make sense in light of sexual selection for female fertility.

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Section 2
Sexual Selection: Male Display and Female Choice

Cooperation decisions are biased by attractiveness, part of this is a 'halo' effect such that we assume more attractive people to be better people.

Chapter 4: Data is presented such that men pay attention to female attractiveness over and above the 'halo' effect and display increased cooperation toward more attractive women.

Chapter 5: Women seem to be equally affected by a male and female attractiveness 'halo' when making trust decisions, however while female participants were also more likely to reciprocate with attractive females, male attractiveness related positively to exploitation of trust. It appears that women recognise male trust as being an offer of ongoing interaction rather than actual trust and the female response is, at least in part, a signal of acceptance or rejection (maintaining reciprocity with less attractive males).

Chapter 6: In an explicitly dating context female participants show a similar pattern of decisions to those they make in trust games. This lends support to the interpretation that female participants recognise male display in the form of 'trust' and choose to reciprocate with an acceptance signal of their own.

Chapter 4

Male Display in Trust Games

Abstract: Prior research has shown that men in better physical quality (more attractive or more symmetrical) show less cooperation in economic games. Two explanations have been hypothesised for this, either lower quality men (a) have greater need to display cooperation in order to attract mates or (b) have greater need of strategic alliance to secure resources. We explored how male self-rated physical dominance interacted with counterpart sex and counterpart attractiveness in Trust Games. Male participants played Trust Games with strangers (with standardised neutrally posed facial images of counterparts). This provided two measures of cooperative behaviour; trust and reciprocation. We find that males cooperate in the Trust Game as a sexual display; cooperation is modulated by female more than male attractiveness. When comparing men reporting high physical dominance with those reporting low physical dominance we found support of hypothesis (a) higher physical dominance predicted less sexual display when making trust decisions and in support of hypothesis (b) more physically dominant men showed less reciprocation toward male counterparts. In conclusion, our results show that male Trust Game decisions are modulated both by sexual display and strategic alliance considerations and that these both interact with male quality.

A factor that modulates male behaviour in economic games is physical quality. Men with low fluctuating asymmetry make lower Ultimatum Game offers (Zaatari & Trivers, 2007) while men rated as more physically attractive are less cooperative in Prisoner's Dilemma, Allocator Choice, Faith, as well as in Trust Games (Takahashi, et al., 2006). We explored reasons for this relationship between physical quality and reduced cooperation using the Trust Game.

Two explanations for the variation in male behaviour are put forward by Zaatari and Trivers (2007). The first is that better quality males need display less pro-social behaviour in order to gain mates; Cooperation is aimed at sexual display. That males display prosocial behaviour in order to obtain sexual access fits well with theories of sexual selection and parental investment (Andersson, 1991; Gangestad & Simpson, 2000; Trivers, 1971). Males under this interpretation are displaying their resources and their willingness to invest in order to elicit female attention and thereafter possible reproductive access. Females are likely to trade-off between physical quality (as a proxy for good genes) and beneficial behavioural traits (such as cooperation) when assessing mates. Males with better physical quality need therefore to display less cooperation in attracting mates and are therefore less cooperative.

The second explanation for reduced cooperation in males with better physical quality is that males are likely to vary in their need for cooperation in obtaining resources; stronger, more able males gain less from a strategic alliance than do weaker less able males. Men with better physical quality may have “superior ability in obtaining resources, especially in situations involving aggression” (Zaatari & Trivers, 2007). As better quality men may be able to use aggression and coercion

more easily they would have less need of strategic alliances and would therefore be less cooperative. Our experimentation was aimed at exploring these two explanations of male behaviour.

Male behaviour in financial contexts has been demonstrated to be biased by sexual factors. When offered a choice between a sum of money now or a larger sum of money next week, men who are shown pictures of attractive women are more likely to discount the future and take the money now (Wilson & Daly, 2004). Similarly, when offered the chance to make donations to charity, men who are observed by an attractive woman are significantly more likely to make more generous donations (Iredale, et al., 2008). Male behaviour is also influenced by sexual factors in economic games. In ultimatum games, while women make equal offers to male or female counterparts, men offer more to female than to male counterparts (Saad & Gill, 2001). Male behaviour is also influenced by possible proceptive sexual cues in that they are more influenced by smiles than female participants while additionally trusting opposite sex counterparts with more money than same-sex counterparts (Scharlemann, Eckel, Kacelnik, & Wilson, 2001). Over and above all of this, men are influenced by more specifically reproductive factors while making economic decisions in that men have also been shown to give greater amounts of money to ovulating females in lap-dancing establishments (Miller, et al., 2007).

Of course, financial behaviour is also modulated by counterpart attractiveness irrelevant of sex; more attractive people get more cooperation (Solnick & Schweitzer, 1999; Wilson & Eckel, 2006). This effect appears to be both because participants expected more attractive counterparts to be more cooperative, i.e. a

'halo' (See Eagly, Ashmore, Makhijani, & Longo, 1991; Langlois, et al., 2000), but also, when expectations of cooperation are statistically controlled, participants prefer to interact positively with better looking people even when they were expected not to cooperate (Mulford, et al., 1998). This was true of both male and female participants. While it may be possible to interpret this as an aesthetic preference for interaction with beautiful people rather than anything explicitly sexual, if male participants are sexually displaying their prosocial credentials we should expect male altruism to be modulated by an 'aesthetic preference' for female attractiveness more than for male attractiveness.

From the forgoing we therefore expected behaviour in our games to replicate effects from: male quality, sex of counterpart and attractiveness of counterpart. To summarise: (a) more dominant men would be less cooperative; (b) participants would cooperate more with female counterparts and (c) participants would cooperate more with attractive counterparts. However, we also expected interactions between these effects. The nature of these interactions should allow us to decide between the hypothesised explanations posited by Zaatari and Trivers for reduced cooperation in better quality males.

While it seemed likely to us that men use cooperation to both display their sexual appeal and in order to gain alliances we considered which of these two motivations to cooperate explain the modulating effect of physical quality on male behaviour. The parameter that is crucial in differentiating between these is counterpart attractiveness.

If males are showing cooperation as a sexual display there are two main predictions from counterpart attractiveness. The first prediction is due to the structure of the Trust Game. A 'halo' effect from attractiveness only has scope where participants make predictions about counterpart behaviour. As the 'reciprocation' decision is the ending move in the Trust Game there is little scope for a 'halo' in this role. We therefore expected a 'halo' in 'trust' decisions but not in 'reciprocation' decisions. We therefore predicted that (1) male counterpart attractiveness would affect participant behaviour only in the 'trust' role whereas female counterpart attractiveness would affect participant behaviour in both Trust Game roles. The second prediction, previously discussed, was that (2) female counterpart attractiveness (as a sexual "aesthetic preference") would be more predictive of male cooperation than male counterpart attractiveness in both trust and reciprocation.

If males are showing cooperation for strategic alliance male counterparts should be more important for this than female counterparts and therefore participants would trust and reciprocate more with male than with female counterparts. Counterpart attractiveness may be seen as a 'halo' in 'trust' decisions but is likely to have little effect in 'reciprocation' decisions.

How these effects interact with male quality is complicated. Our predictions here are that individuals will focus their effort where it best serves their interests. In playing the Trust Game effort might be expended evaluating trustworthiness but might equally be expended evaluating mate value or strategic alliance value. Therefore if, as we predict, male behaviour is modulated by the sex and (female) sexual attractiveness of their counterparts we should also expect a further interaction with

participant quality. If the first explanation from Zaatari and Trivers (2007) is correct, cooperation is a sexual display, we should find lower quality males to be more motivated to make decisions about sexual display i.e. female attractiveness should modulate decisions of lower quality males more than higher quality males. On the other hand, if as also suggested by Zaatari and Trivers (2007) the relevant explanation of male behaviour is strategic alliance we should find that lower quality males make more effort in strategic alliance decisions than higher quality males i.e. lower quality males will make more decisions to cooperate with males.

Experiment: Trust Game (Male Display)

Participants

32 male participants were recruited from students at the University of St Andrews. Given the nature of our hypotheses, data from two participants reporting non-heterosexual sexual preferences were excluded from the analysis. The data from 30 male participants (mean age = 21.1, s.d. = 1.21) who took part in a 'two-person' binary choice sequential Trust Game is reported below.

Images

50 males and 50 females (white; aged 18-25) were photographed in neutral pose. Forty one participants (17 male/24 female; mean age = 21, s.d. = 3.29) rated the facial images for attractiveness on a Likert-type scale of 1–7. Images were masked (to exclude hair and clothing) and presented in random order. The attractiveness of each facial image was calculated as the mean rating for that face across all participants. The reliability of attractiveness ratings was very high (Cronbach's $\alpha > 0.9$).

Experiment Procedure

We used a binary choice version of the Trust Game as outlined in Chapter 1.

Participants were photographed and were informed that the outcomes of their games would be dependent upon the previous behaviour of the individuals in the photographs and that their final payment for the games would be equivalent to the outcome of one of the games they played.

Participants were given written instructions on how the game was played (see Appendix 1) and a flow chart of the game was present on screen throughout (See Appendix 2). Before the game started participants ran through a number of examples to familiarise them with the possible decisions and outcomes in the game.

The only information available about their counterpart for each game was a facial image masked to exclude hair and clothing.

The previously rated facial images 50 male and 50 female were used for game play. Images were split by sex in to two blocks of games. Within each block participants played with half of the images as player one and half as player two with additional 25 blank filler images as counterparts who chose not to trust the participant. The blocks were presented in randomised order and games within each block were also presented in randomised order.

The outcome of each game was decided by participants where they were player 2 and were randomised biased to previous play for games where participants trusted as player 1 (e.g. if counterpart previous reciprocated 90% there would be a 90% chance of reciprocation).

Self-rating

Participants stated how much they agreed with the following statement on a Likert-type scale of 1 to 7: “If you were engaged in a physical fight with a same-sex peer, you would probably win.” (from Puts, Gaulin, & Verdolini, 2006).

Analysis

Data was analysed only from individuals reporting heterosexual preference. Facial images were previously rated for attractiveness as described above. Facial images were ranked by rated attractiveness and split into groups of the 12 most and 12 least attractive group, discarding the median images. Participants played trust or reciprocation game roles with faces that were split for analysis into male or female, and high or low attractiveness.

Eight scores were calculated for each participant; Four scores for ‘trust’ decisions calculated as the proportion of trust decisions made with the 12 most attractive and with the 12 least attractive male images and the same proportions with the 12 most and least attractive female images. Four scores were also calculated for these 12 image groups for ‘reciprocation’ decisions as well.

Self-rated dominance and attractiveness were split at the means, both of which were between 4 and 5, scores of 1-4 were therefore treated as low and 5-7 were as high.

Results

Participants chose to trust 46% of their counterparts and reciprocate with 68% of their counterparts. They trusted female counterparts more often than male (Paired t-test: $t_{30} = 2.7$, p = 0.012; see Fig. 4-1) and reciprocated more often with male counterparts than female (Paired t-test: $t_{30} = 2.5$, p = 0.02; see Fig. 4-1).

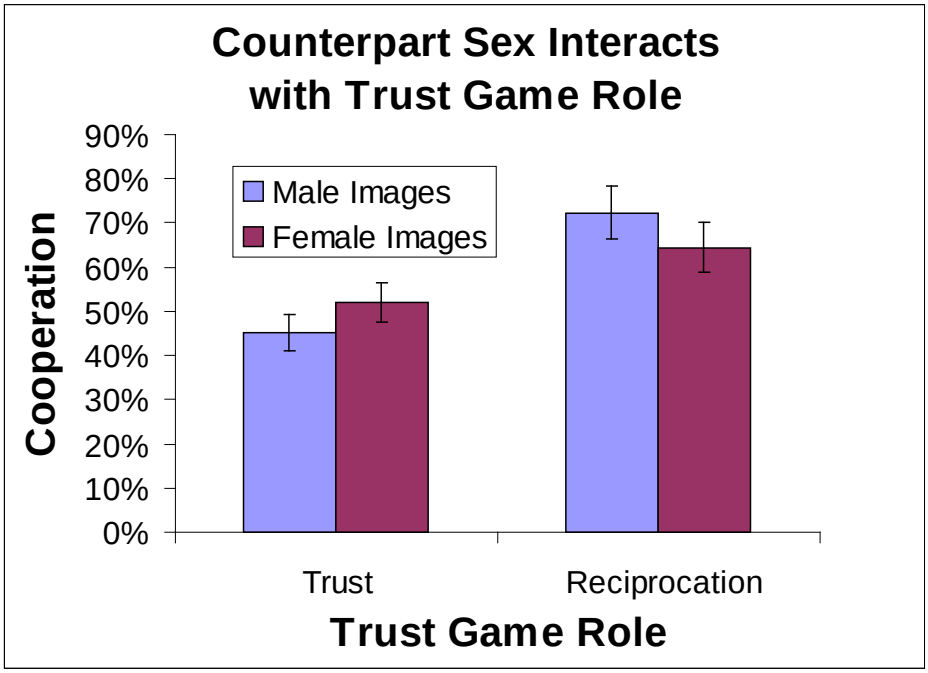


Figure 4-1 – Male players 'trust' females and 'reciprocate' with males. Male players trusted female counterparts more often and reciprocated with male counterparts more often.

Hypotheses were tested by mixed 3 way ANOVA with the within participant factors: sex of image (2 levels), image attractiveness (2 levels) and the between participant factor self-rated dominance (2 levels).

Player one: Trust decisions

The ANOVA revealed a main effect from the attractiveness of the images on trust judgments, (ANOVA: $F_{1,24} = 30.2$, $p < .0005$, Fig. 4-2). More attractive individuals were more trusted. Additionally, there was a main effect from the sex of the images, (ANOVA: $F_{1,24} = 4.4$, $p = .046$, Fig. 4-2). The male players invested more trust in female images. There was also a significant interaction between attractiveness of the image and the sex of the image (ANOVA: $F_{1,24} = 5.4$, $p = .03$, Fig. 4-2) Male players trust decisions were more affected by female attractiveness than by male attractiveness. There was no significant difference in t-test between male (mean = 2.04) and female (mean = 2.09) images in rated attractiveness (p = .34).

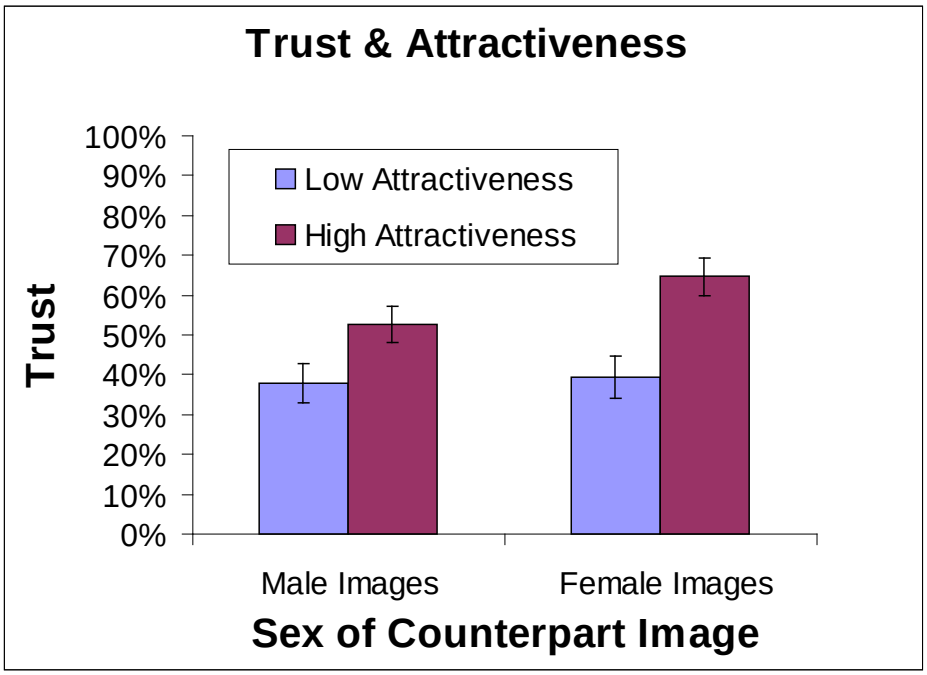


Figure 4-2 – Sex, facial attractiveness and proportion of trust judgements. Players trusted attractive more often than unattractive images (ANOVA: $F_{1,24} = 30.2$, $p < .0005$) and female more often than male images (ANOVA: $F_{1,24} = 4.4$, $p = .046$). Players' trust was also more affected by female attractiveness than by male attractiveness (ANOVA: $F_{1,24} = 5.4$, $p = .03$).

Self-rated dominance had no effect on the overall proportion of faces trusted (ANOVA: $F_{1,24} = 1.1$, $p = 0.3$) but there was an interaction between sex of image, attractiveness and self-rated dominance (ANOVA: $F_{1,24} = 5.1$, $p = .034$, Fig. 4-3). The less dominant males showed greater sensitivity to female attractiveness than did the more dominant males but for male faces the effects of attractiveness were equivalent.

We further explored this result by running 2-way ANOVAs separately for the 2 dominance groups. Less dominant participants showed a main effect of attractiveness (ANOVA: $F_{1,9} = 6.5$, $p = 0.03$), no effect of sex of face (ANOVA: $F_{1,9} = 1.8$, $p = 0.2$) and a sex of face by attractiveness interaction (ANOVA: $F_{1,9} = 10.6$, $p = 0.01$, Fig. 4-3). The more dominant men also showed a main effect from attractiveness (ANOVA: $F_{1,15} = 36.0$, $p < 0.0005$) but no effect from sex of face

(ANOVA: $F_{1,15}$ = 2.9, p = 0.11) and no interaction between sex of face and attractiveness (ANOVA: $F_{1,15}$ = 0.04, p = 0.95, Fig. 4-3).

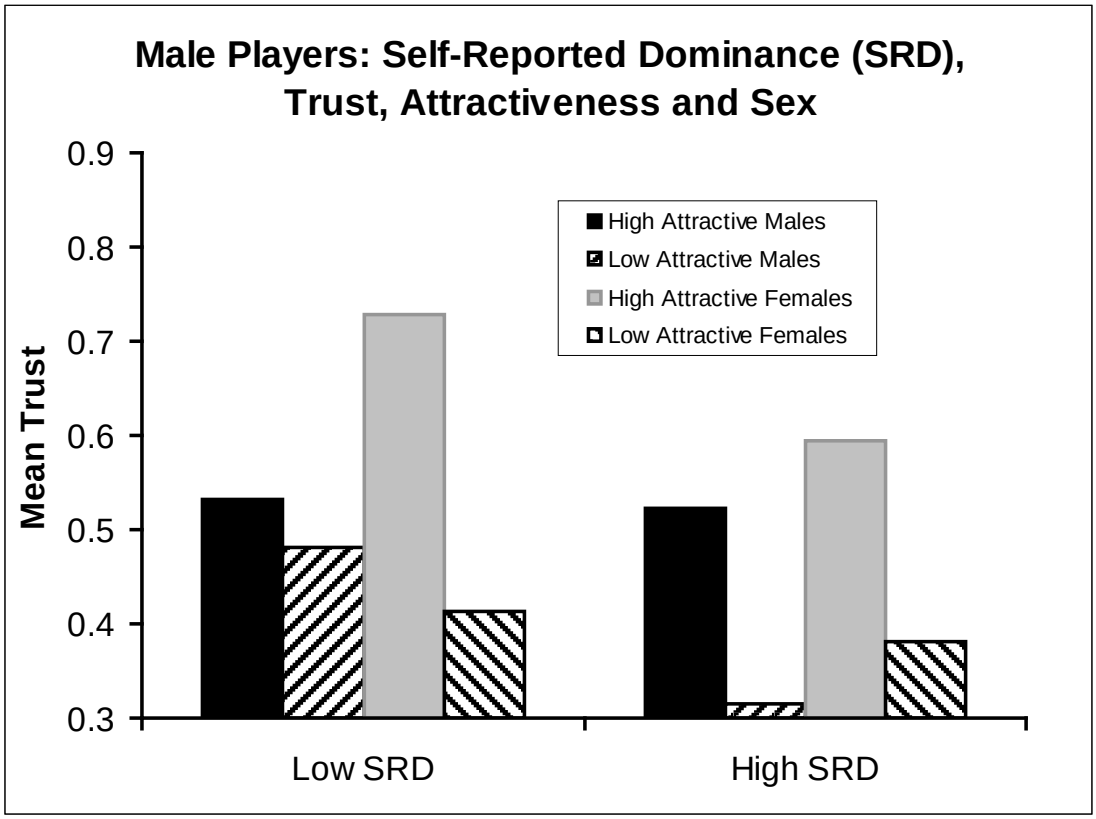


Figure 4-3 – The effect of self-reported dominance on proportion of faces trusted. Less dominant males were more affected by female than male attractiveness ($F_{1,9}$ = 10.6, p = 0.01) whereas more dominant males were not more affected by female attractiveness ($F_{1,15}$ = 0.04, p = 0.95).

Player two: Reciprocation

Participants showed a main effect with more attractive images eliciting more reciprocation from male game play (ANOVA: $F_{1,24}$ = 11.0, p < .005, Fig. 4-4). A main effect from the sex of image was also seen (ANOVA: $F_{1,24}$= 10.5 p = .004, Fig. 4-4). Male participants reciprocated more with male image counterparts than with female. Image sex and attractiveness interacted, however, such that while more attractive images elicited more reciprocation overall this did not appear to be true of the male images (ANOVA: $F_{1,24}$ = 13.2 p < .005, Fig. 4-4). Tested separately there was no effect of male image attractiveness on reciprocation decisions (Paired t-test: t_{26} = 0.45, p = 0.65).

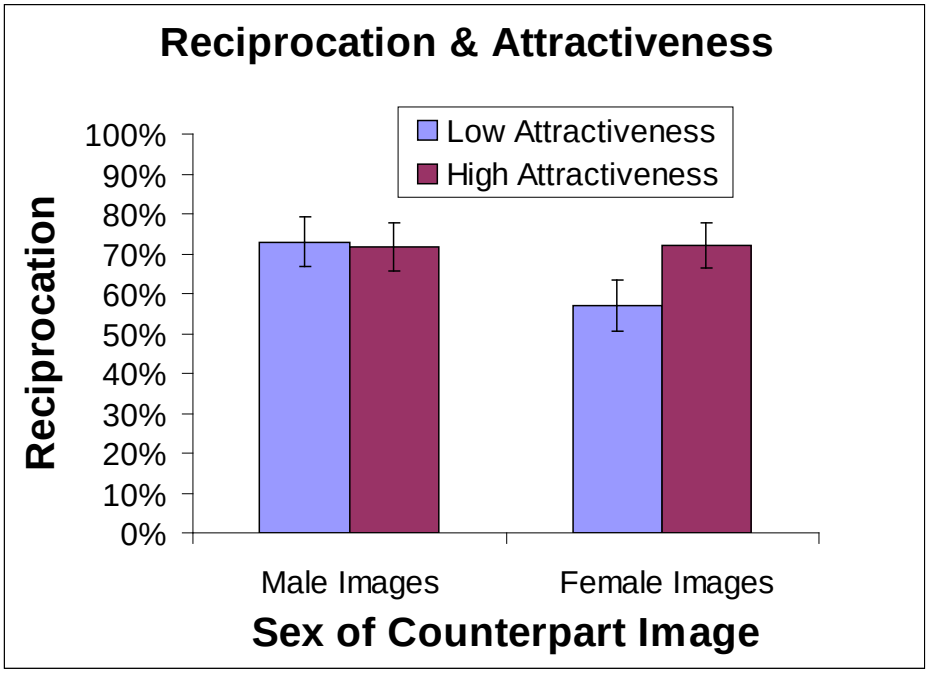


Figure 4-4 - Effects of sex and facial attractiveness on proportion of reciprocation judgements. Players reciprocated more often with more attractive counterparts (ANOVA: $F_{1,24} = 11.0$, $p < .005$) but an interaction with sex of image showed this to be driven by female attractiveness (ANOVA: $F_{1,24} = 13.2$ $p < .005$). Additionally, male participants showed a preference to reciprocate with male rather than female counterparts (ANOVA: $F_{1,24} = 10.5$ $p = .004$).

Self-rated dominance had no effect on the overall proportion of reciprocation (ANOVA: $F_{1,24} = 0.76$, $p = 0.39$) but interacted with sex of image such that less dominant males showed a greater preference for reciprocation with male images (ANOVA: $F_{1,24} = 4.7$ $p = .04$, Fig. 4-5). There was no interaction between sex of image, attractiveness and self-rated dominance (ANOVA: $F_{1,24} = 1.8$, $p = 0.2$). The low dominant males did not show greater sensitivity to female attractiveness than the high dominant males when making reciprocation decisions.

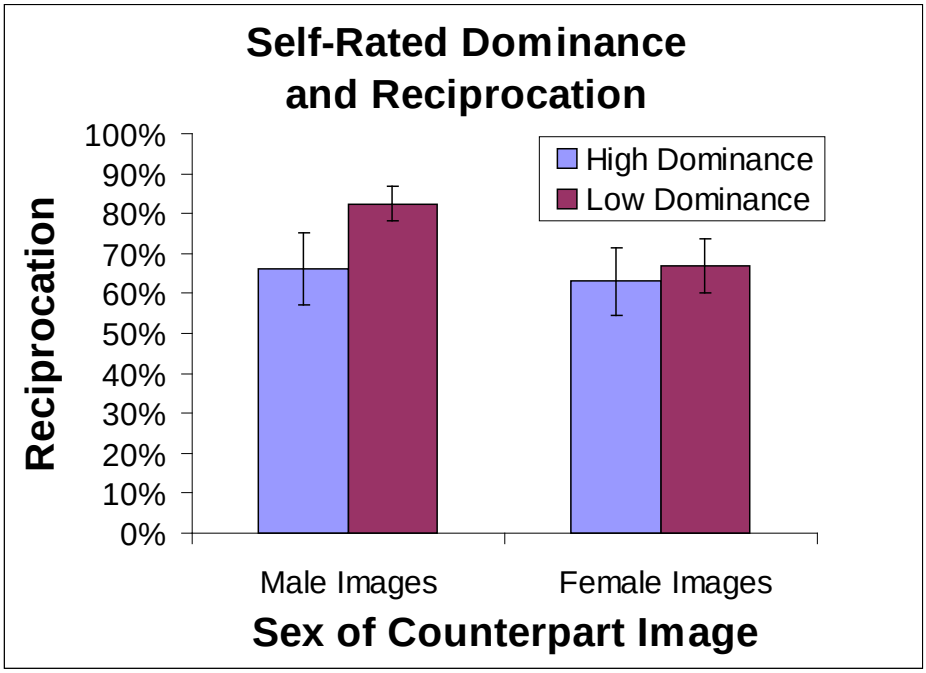


Figure 4-5 – The effect of self-reported dominance on proportion of faces shown reciprocation. Less dominant males showed a greater preference for reciprocation with male images (ANOVA: $F_{1,24} = 4.7$ $p = .04$).

Discussion: Men 'Display' Trust

Participants showed a clear tendency in the Trust Game to cooperate as a sexual display in two ways. First, female attractiveness always elicited more cooperation than male attractiveness and second, where attractiveness effects could not be explained as a 'halo', female attractiveness (but not male) modulated cooperation.

While physical dominance did not predict overall trust and reciprocation it did interact with the other variables. Trust decisions were more influenced by female attractiveness among the less dominant males than the more dominant males. The less dominant males were also more likely than more dominant males to reciprocate with counterpart males.

The differing moderating effects of physical dominance between Trust Game roles may be explained by the different payoff structure between those roles. The two roles have different social valences. While the trust decision is somewhat ethically

neutral and based in expectancies of behaviour a negative reciprocation decision is exploitative and may run contrary to social norms (Hardin, 2002). Also, a decision to trust is a decision to initiate an interaction whereas the reciprocation decision is taken in response to such an initiation.

Trust in the form of sexual display is relatively low cost and possibly high payoff, if the male can attract the attractive female counterpart, and females may value cooperative behaviour over good genes. Trust as initiation of social alliance although similarly low cost is less likely as high payoff. Although, less dominant males are less discriminating over male counterpart attractiveness, perhaps soliciting alliance with males they suspect are untrustworthy.

Reciprocation as sexual display plays out here as exploitation of less attractive female counterparts and is behaviour seen equally in more and less dominant males. Reciprocation as alliance seeking behaviour is clearly seen as the less dominant males cooperate with males that have initiated an interaction.

In our data there are significant main effects on participant trust and reciprocation from both counterpart sex and attractiveness. In partial support of Takahashi and colleagues it is clear that our male participants trust female counterparts in order to impress these females with their social altruism, at least in part. Equally clearly, in support of Zaatari and Trivers, is that better quality males are less reciprocating because they have less need for strategic alliance: in the case of physically dominant males, they have less need of alliance with other males, and for more attractive males, they have less need of alliance with anyone.

The original trust games carried out by (Berg, et al., 1995) showed no difference between roles but, opposite to our data, it is typical for players to show more trust than reciprocation (cf. Henrich, et al., 2004). It is likely that our participants responded to the presence of the on-screen faces as the mere presence of abstract 'eyespots' on screen can increase cooperation in anonymous economic games (Haley & Fessler, 2005) similarly, the presence of identity information dramatically increases both trust and, particularly, reciprocation behaviour to similar levels shown by our participants (Huck, et al., 2007).

Effects of counterpart sex on male behaviour in economic games has been demonstrated previously (Saad & Gill, 2001) as have attractiveness effects (Mulford, et al., 1998; Solnick & Schweitzer, 1999; Wilson & Eckel, 2006). A result here that to our knowledge is previously unreported is that these effects also interact such that female attractiveness has a stronger effect than male attractiveness upon male decisions.

The modulating effect of self-reported physical dominance was such that more dominant males treated male and female attractiveness equivalently for trust decisions whereas less dominant males preferentially trusted attractive female counterparts. A similar modulating effect on trust was observed from self-rated attractiveness. Less attractive participants (compared with more attractive participants) were more likely to trust attractive women.

These results are equivocal in deciding between the two explanations for male differences. Male trust decisions provide evidence for sexual display because more dominant (and probably more attractive) males show less concern to trust the

attractive females. Male reciprocation decisions, however, suggest strategic alliance motivations because less dominant males reciprocate more often with male counterparts and more attractive males reciprocate less with all counterparts. At the same time there is a modulation of the sex of face by attractiveness interaction from neither physical dominance nor male attractiveness.

It should be noted that the measure of cooperation used by Zaatari and Trivers (Zaatari & Trivers, 2007) were ultimatum game offers and the measures that Takahashi and colleagues (Takahashi, et al., 2006) used were the Prisoner's Dilemma and continuous versions of the Allocator Choice, Faith, and Trust Games. These measures, especially the ultimatum game offers, are all more similar in kind to the reciprocation stage of our binary Trust Game and as such may be best explained as male variance in strategic alliance decisions rather than sexual display but further experimentation would be required to confirm this.

It is also interesting to note while highly physically dominant men may have better access to resources where it is dependant on interactions with men, i.e. possibly aggressive or competitive interaction, this may not be as true of male interactions with women. Highly attractive men, on the other hand, may have advantages in all social interactions.

In summary, our results support the idea that male participants in Trust Games display cooperation to females as a sexual display. There is evidence that male quality may modulate sexual display in trust decisions but that male quality modulates strategic alliance considerations in reciprocation decisions. Higher quality men reciprocate less as they have less need of cooperation.

In the next chapter we turn to female Trust Game behaviour that suggests that this male display is recognised as a display.

Chapter 5

Female choice in Trust Games

Abstract: Male financial behaviour has been shown to be modulated by sexual factors, even in exclusively financial contexts. While female financial behaviour is influenced by sexual factors in explicit courtship contexts such influences have not been shown in non-sexual contexts. We explored the influence of attractiveness on the financial behaviour of females in the context of the trust game, focusing on male facial attractiveness. Facial attractiveness of both sexes predicts female trust behaviour. Facial attractiveness also predicts reciprocation behaviour, however while female facial attractiveness predicts positive reciprocation, female participants exploit the trust of attractive males more often than unattractive males. Participants are also less likely to reciprocate with males than females. These results are consistent with the notions that females: (a) recognise that male financial 'trust' is in part sexually motivated and, (b) exploitation of that 'trust' is indicative of social or sexual interest in males.

From the last chapter we have seen that men are influenced by sexual factors when making decisions that are otherwise non-sexual such as financial decisions. Also as discussed previously these findings about male financial behaviour all make sense in light of sexual selection and conflict over parental investment (Trivers, 1972).

Men have consistent biases to display their generosity and wealth by potential or actual investment in women they consider attractive. Evidence that female behaviour in financial contexts is influenced by such sexual display is sparser.

As mentioned, the theory would predict that women should discriminate between men on the basis of resources and displayed generosity. There is some evidence for this in female self-reports. In surveys of criteria for long-term sexual partners both sexes emphasise items such as mutual attraction, being dependable, emotional stability and kindness, however there are sex differences. Specifically, while men emphasise the importance of physical attractiveness more, women emphasise social status and resource (Buss, 1989). Li et al (2002) found that these sex differences are best understood when contrasting necessary and luxury factors. A minimum of physical attractiveness is necessary in a partner for men but for women a man must have a minimum level of social resource or status. Other items, such as kindness, are very desirable for both sexes but nevertheless are luxuries.

That men display wealth and that women are willing recipients of gifts is not surprising. It is clear that gift-giving is a feature of human courtship (Greer & Buss, 1994; Griskevicius et al., 2007; Hawkes, 1993; Hawkes & Bliege Bird, 2002; Huang, 2000; Iredale, et al., 2008; Jonason, Cetrulo, Madrid, & Morrison, 2009; Miller, 2007; Miller, et al., 2007; Saad, 2006; Sanderson, Keiter, Miles, & Yopyk, 2007). The

question we wished to explore here was whether this aspect of female behaviour would generalise to non-sexual contexts. If men are biased to both display wealth and invest in women to such an extent that it influences their behaviour in the Trust Game it is possible that women should be biased to treat these displays as displays and preferentially show willingness to accept them from desirable prospective partners. To this end we had female participants play Trust Games with counterparts varying in sex and attractiveness.

As behaviour within gender roles is circumscribed it is not enough to find that women show differential behaviour toward the sexes we also need to consider the effects of attractiveness on behaviour.

If women have a bias to interpret male generosity with money as courtship effort there will be a difference between the effect of counterpart attractiveness on participant's trust and reciprocation decisions. Trust decisions will be unaffected by this bias. Reciprocation decisions with female counterparts should also be unaffected by this bias. Decisions whether to reciprocate or exploit male trust, however, may be a decision whether to accept his investment and as such female participants should prefer to accept investment from more attractive male counterparts.

From this we predicted two things about the effect of counterpart attractiveness. First, that a 'halo' effect would increase cooperation in all conditions (particularly trust decisions as discussed in Chapter 3). Second, that participants would reciprocate less with attractive male counterparts (i.e. accept investment).

Experiment: Trust Games (Female Choice)

Participants

74 female participants were recruited from an undergraduate psychology class at the University of St Andrews. Data was restricted to heterosexual participants (N = 70, mean age = 21.1, s.d. = 1.81).

Images

50 males and 50 females (white; aged 18-25) were photographed in neutral pose. Forty one participants (17 male/24 female; mean age = 21, s.d. = 3.29) rated the facial images for attractiveness on a Likert-type scale of 1–7. Images were masked (to exclude hair and clothing) and presented in random order. The attractiveness of each facial image was calculated as the mean rating for that face across all participants. The reliability of attractiveness ratings was very high (Cronbach's $\alpha >$ 0.9).

Experiment Procedure

The binary choice version of the Trust Game as outlined in Chapter 1 was used.

The protocol followed was exactly as in Chapter 4.

Analysis

Facial images were previously rated for attractiveness as described above. Facial images were ranked by rated attractiveness and split into high and low groups. Participants played trust or reciprocation game roles with faces that were split for analysis into male or female, and high or low attractiveness.

Eight scores were calculated for each participant; Four scores for 'trust' decisions calculated as the proportion of trust decisions made with the 12 most attractive and with the 12 least attractive male images and the same proportions with the 12 most

and least attractive female images. Four scores were also calculated for these 12 image groups for 'reciprocation' decisions as well.

Self-rated attractiveness was split at the mean (mean = 4.01), scores of 1-4 were treated as low attractiveness and 5-7 as high attractiveness.

Results

Participants trusted 48% (range = 14% to 98%, SD = 14%) of their counterparts and reciprocated with 72% (range = 4% to 100%, SD = 20%) of their counterparts.

Player one: Trust decisions

Predictions were tested by 2-way ANOVA with the factors: sex of image (2 levels) and attractiveness (2 levels).

Participants showed a significant main effect from the attractiveness of the images ($F_{1,69} = 65.2$, $p < .0005$, see fig. 5-1). More attractive individuals were more trusted. However, as predicted there was no significant effect from the sex of the images ($F_{1,69} = 2.9$, $p = .10$) nor any interaction between image sex and attractiveness ($F_{1,69} = 0.3$, $p = .59$). Female participants are equally affected by attractiveness with both male faces and female faces (Fig. 5-1).

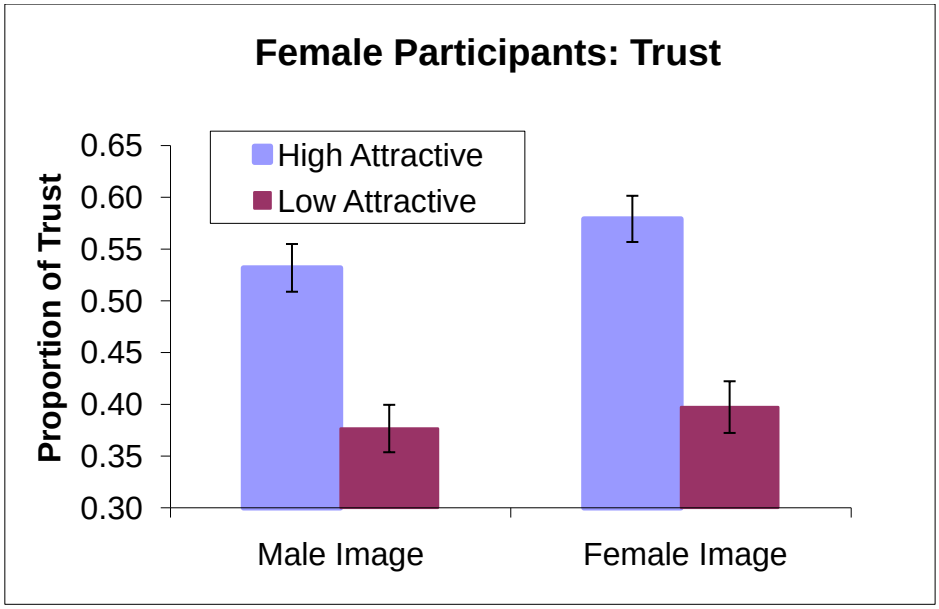


Figure 5-1 - Participants trust attractive faces. Participants trust attractive faces but show neither significant sex preference nor any sex dependant response to attractiveness.

When including self-rated attractiveness in the analysis as a between subject factor previous effects are found with no moderating effects from self-ratings (all $p > .47$).

Player two: Reciprocation

Hypotheses were tested by 2-way ANOVA with the factors: sex of image (2 levels) and attractiveness (2 levels).

Main effects were found from the sex of image ($F_{1,69} = 4.1$ $p = .048$, see fig. 5-2) and image attractiveness ($F_{1,69} = 11.6$, $p < .005$, see fig. 5-2). However, these also interact ($F_{1,69} = 40.3$ $p < .0005$, see fig. 5-2). While more attractive images elicit more reciprocation overall, this is true when considering female faces alone ($t_{70} = -6.5$, $p < 0.0005$). For male images, the opposite is true; low attractive male faces elicit more reciprocation than attractive male faces ($t_{70} = 2.5$, $p = 0.013$). The high attractive group of male faces is also made from a set of faces which are rated significantly more masculine, healthier and more trustworthy than the low attractive group. This

runs counter to an interpretation that females may avoid threat of punishment or expect untrustworthiness from more attractive male counterparts.

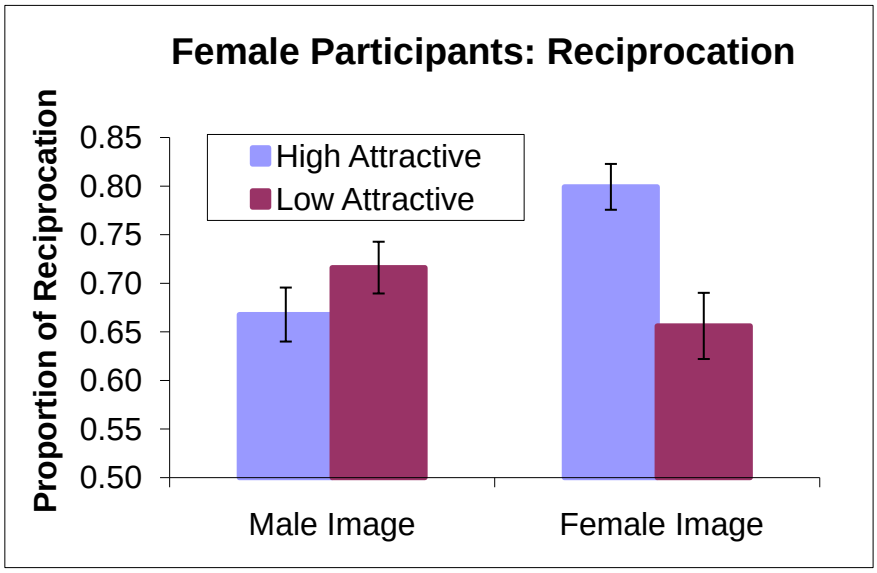


Figure 5-2 - Participants exploit trust from attractive males but not from attractive females
Women reciprocate more with female counterparts and with more attractive counterparts. However, this is qualified by an interaction. Male attractiveness elicits less reciprocation.

When including self-rated attractiveness in the analysis as a between subject factor previous effects are found with no moderating effects from self-ratings (all $p > .45$).

Discussion: Women Exploit the Trust of Attractive Men

As we predicted, participants in our trust games were influenced by an attractiveness 'halo' and were significantly more cooperative with more attractive counterparts. However, while we predicted that a bias to accept investment from attractive males would moderate this effect we were surprised to observe that the 'halo' effect disappeared and that female participants were significantly more likely to exploit the trust of more attractive males.

Participants increase non-reciprocation with male images compared with female images in support of the interpretation that women respond to male 'trust' as display of wealth and generosity. This interpretation would be tentative were it not

further supported by the fact that women show more exploitation of more attractive male faces than unattractive. It should be heavily emphasised that this is an unlikely result. Attractiveness elicits positive responses and increased cooperation (Langlois, et al., 2000). That our female participants' exploit attractive males rather than reciprocate with them is very surprising.

This result suggests that when playing the Trust Game these female participants perceived some payoff structure outwith the game that is specifically modulated by male attractiveness; in the Trust Game payoff matrix (Table 1-2) there are values of P and Q which intereact with male counterpart attractiveness. We suggest that female participants see male 'trust' as advertising and either exploit it (Q) with the payoff of encouraging further social interaction or reciprocate (P) in order to discourage further social interaction.

As females make greater investment in offspring (Trivers, 1972) and therefore have more to lose in making a poor choice of reproductive partner it is to be expected that evolved female psychology should include mechanisms not only of mate preference and choice but of strategic control of interactions with male strangers (Grammer, 1990). If male 'trust' in these games is used as a signal of interest in attractive females, and this would seem to be the case in the last chapter, it is reasonable to interpret female exploitation of male 'trust' as a reciprocal signal of interest in ongoing social interaction and reciprocation of male 'trust' as a signal of a lack of interest.

In summary, we found that female participants appear to recognise that male 'trust' in Trust Games has at least some component of sexual display and are more likely to

keep the game interaction a fair one with less attractive male counterparts and more likely to exploit more attractive male counterparts (perhaps obligating themselves to further interaction).

We tested this interpretation further by asking participants to make similar decisions within an explicitly sexual context.

Chapter 6

Food sharing and sex

Abstract: Food sharing is commonly practiced in human society as a form of cooperative exchange of resources. Humans also exchange resources during courting to obtain romantic partners out of a competitive mating market. Providing resources is one way a male can increase his ability to attract a female, and food can be a commodity that could be exchanged with a potential mating partner. Studies on other animals have shown relationships between food sharing and sex, and other exchange markets with sex. In this present study, we explored human mating markets in relationship to food sharing by studying payment choices for hypothetical romantic dates. First, we questioned participants about their preference to pay the food bill on a hypothetical dinner date. We then investigated whether any preferences were related to a partner's facial attractiveness, or the participant's perception of their mate value in a mating market (i.e., perceived value relative to others). Our results indicated that female participants preferred male dates to pay more than males preferred females to pay. Females also preferred to have males that had higher facial attractiveness pay for them. In contrast, male participants showed a greater willingness to pay for dates that had higher facial attractiveness. Higher self-rated attractiveness in females was related to preferences for the male to pay, while in males self-rated attractiveness was related to preferences to not pay the entire bill. These results support that the decision to pay for the food bill during a date was influenced by factors related to a person's competitive ability in a mating market. Individuals showed exchange strategies consistent with sexual selection theory and the relative mate quality of themselves and hypothetical partners.

The trade of food from males to females for access to sexual opportunity, be it immediate exchange or a long-term relationship based on a series of exchanges is predicted from sexual selection theory (Darwin, 1871; Kappeler & van Schaik, 2004; Trivers, 1972).

Human beings share food in cooperative exchange relationships, including sexual bonding (Bliege Bird, Bird, Smith, & Kushnick, 2002; Gurven, 2004; Moore, 1984). Men that can provide more food resources in traditional societies tend to be 'showing off' at least in part to attract mating attention (Wood & Hill, 2000) and they tend to be preferred by females as mating partners, and have more offspring (Smith, 2004). There is evidence of a direct meat-for-sex trade in traditional societies such as the Sharanahua (see Gurven, 2004; Siskind, 1973, p. p. 103)

In general, females are attracted to males that can provide resources that will sustain both them and their offspring (Buss, 1989; Trivers, 1972). As a consequence of such trades, human romantic relationships seem to be influenced by the conditions of a mating market where partners are chosen based on their quality as a partner relative to others in the market (Pawlowski & Dunbar, 1999). Males are chosen by females for their ability to provide physical resources, and females are chosen by males for their current reproductive condition and ability to produce and care for offspring (Buss, 1989). Generosity is attractive in both sexes (Farrelly, et al., 2007).

Self-evaluation and market value

Individuals evaluate their own mate value relative to others, and this provides a subjective gauge of their ability to attract a romantic partner. A number of studies

have shown that attractiveness relates to one's ability to obtain romantic dates (De Vries, et al., 2008; Kurzban & Weeden, 2005; Walster, et al., 1966; Woll & Young, 1989). Self-perceived attractiveness should therefore reflect an individual's perception of their mate value. Since we expect market influences to play a factor in mate selection, self-assessment of value should be related to the qualities and individual demands from partners (i.e., more attractive people will be more demanding of their partner).

Attractiveness does seem to affect the qualities individuals seek from a partner. For example, females with lower waist-to-hip ratios that also scored low on measures of anxiety, depression and stress showed a higher preference for male physical indicators of male health (Jones, Little, et al., 2005). Females with lower waist-to-hip ratios and high scores for facial attractiveness showed preferences for more masculine male faces for long-term relationships (Penton-Voak, et al., 2003). Also, self-rated attractiveness in women has been shown to relate to preferences for facial masculinity and symmetry (i.e., attractiveness) in partners (Little, et al., 2001). Lastly, one study demonstrated that female self-rated attractiveness was influenced relative to the attractiveness of female images that they were shown and that this manipulated their preferences of male facial masculinity (Little & Mannion, 2006). Females that observed images of attractive females downgraded their self-evaluation and showed reduced preferences for masculine males. Those who observed unattractive images upgraded their self-evaluation and showed increased preference for masculine males. This effect shows clearly how the immediate market conditions might influence a female's perception of her mate value or competitive ability in a market of other females.

There is little investigation on male self-perceived attractiveness but in one study, according to Little et al. (personal communication), males showed increased preference for female facial femininity if they consider themselves to be more attractive. It has also been argued that high-quality males are less likely to invest in mates and instead pursue a strategy of maximising their number of lifetime mates (Gangestad & Simpson, 2000). This is supported in that more physically attractive males are more likely to have more short-term sexual relationships than less attractive males (Rhodes, et al., 2005). As with females, it seems the self-evaluation of males can influence how they select and invest in female partners in a mating market

In the present study, we used sexual selection and market theory to generate several predictions about male and female preferences for who will pay for the food following a dinner date (i.e., provide and share the food). Based on sexual selection theory, women should be more selective and therefore we expect females to prefer males to pay for dates and males to be more willing to pay than females.

Also, individuals should evaluate their potential partners based on attractiveness, as a possible cue of genetic quality. Therefore, we expect that attractiveness will influence preferences. We expect men to prefer to pay for the meal with more attractive females, and women will be more likely to test attractive males to determine their ability and willingness to provide resources. We predict women will be less interested in unattractive males and therefore, females might refrain from engaging in any exchanges that might communicate the possibility of romantic interaction. In compensation for this, these males should be more willing to pay for

the date in an effort to establish an exchange. Lastly, attractive females will capitalize on the market and be more likely to request resources i.e. prefer others to pay, as they are more likely to be able to acquire them from a male.

These predictions allowed us to test whether preferences for providing food on a date were related to relative partner value in a mating market. Since our data was collected from hypothetical cases though, we did not evaluate actual food-mating exchanges. Consequently, we were not able to test the outcome of food provisioning exchanges on human mating, only the preferences surrounding them.

Experiment: Payment Preferences on Dates

Participants

A total of 2,280 participants took part in an online experiment, of which we included only participants who (a) completed all parts of the experiment and (b) reported that they had taken the time to answer questions honestly. Also, as we are interested in mating behaviour we included only participants who (c) were heterosexual, and (d) were clearly of reproductive age; within an age range of 20 to 35 years old. This reduced the number to 245 male [mean age = 26.2(S.D. 4.5) years] and 171 female [mean age = 25.2(S.D. 4.4) years] participants.

Procedure

After giving consent, participants filled in a basic demographic questionnaire including age, sex and sexual orientation. They were asked to rate how attractive they considered themselves to be on a Likert-type scale of 1 = very unattractive to 7 = very attractive. Participants were then given the following instructions:

> "You will now be shown a series of facial images in two blocks. You should imagine that you have been out for

> a meal with the individual in the photograph. There are then three options for paying the bill at the end of the meal. You have to decide what you would prefer: to pay for both of you, to split the bill in half or for the other person to pay for the meal."

We presented participants with 12 opposite sex facial images (in randomised order) and asked who they would prefer to pay the bill.

Stimuli

Each image presented was a composite of 3 same sex facial photographs (See Tiddeman, Burt, & Perrett, 2001 for computer graphics techniques). The composite images were made from images selected from a set of neutrally posed images [50 male and 50 female – age 20.4(S.D. 1.6) years].

The composite images were ranked for attractiveness by 28 participants [age 21.6(S.D. 4.4) years; 10 male/18 female; Cronbach's alpha > .93] who were not otherwise included in this study (see Figure 6-1 for composite images and final ranking).

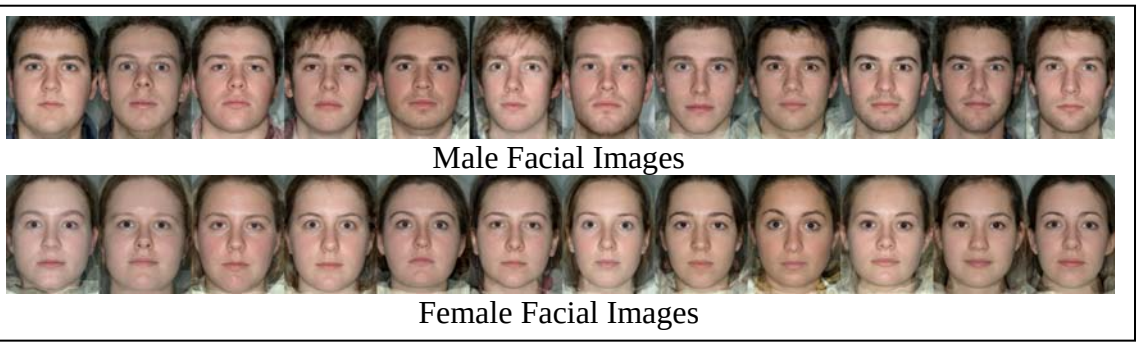


Figure 6-1 – Stimuli images ordered left to right for attractiveness.

Analysis

For each image the participants had to answer how they would prefer the bill for the hypothetical meal to be paid. Answers were scored as -1 = other pays, 0 = split the bill and 1 = participant pays for the meal.

Spearman's correlations were calculated between participant's self-reports and mean scores and between mean responses elicited by images and image attractiveness rank.

To test for interactions between image attractiveness and participants' self-reported attractiveness we split the images and participants by sex and analysed the participant preferences for payment by mixed ANOVAs with three levels of the within-subject variable (i.e. mean response to four least attractive images, four most attractive and the four middle images) and three levels of the between-subject variable (i.e. self-rated attractiveness).

As the participant self-rated attractiveness variable was negatively skewed, participants were allocated to three attractiveness levels; self-rated attractiveness values of 1-4 were allocated to the low-attractiveness group (male: 81; female: 59), a rating of 5 to the mid-attractiveness group (male: 92; female: 63) and a self rating of 6 or 7 to the high-attractiveness group (male: 71; female: 49).

Results

Most often participants preferred to split the bill (58%) and both sexes report a mean preference not to pay for the meal, -0.4(S.D. 0.35) for females and -0.07(S.D. 0.46) for males. Still, female participants preferred the opposite sex to pay for the meal more often than males, indicating a significant sex difference in choice (Mann-Whitney: $U_{171, 245} = 12085$, $p < .0005$, see Fig. 2). Our results show that neither sex prefers to pay the bill, but that females have a higher tendency to prefer meals to be paid by their date.

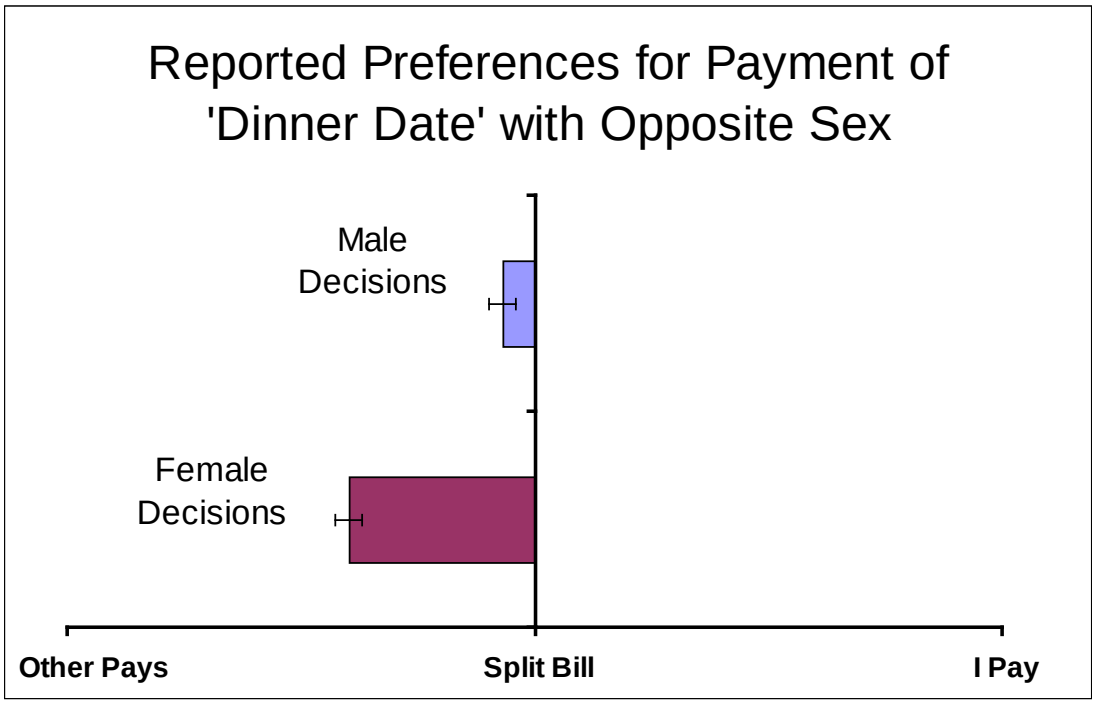


Figure 6-2 - Sex difference in payment preference for 'dinner dates.' Females show a stronger preference than males for the opposite sex to pay for the meal.

Self-Rated attractiveness and payment

Participants' mean reported preference correlated with the participants' self-rated attractiveness (Male: r_s = -.13 N = 244, p = .046; Female: r_s = -.17 N = 171, p = .026). The self-rated attractiveness of participants of both sexes was related to preferences for the opposite sex to pay for the meal.

Image attractiveness and payment

The mean reported preference for each image correlated with image attractiveness rank.

Female image attractiveness rank strongly correlated with the average reported male preference to pay for the dinner date (Spearman's rho: r_s = .90, N = 12, p < .0005). Men more frequently preferred to pay for dates with more attractive females.

Male image attractiveness negatively correlated with the mean female reported preference to pay for the dinner date (Spearman's rho: $r_s = -.80$, N = 12, $p < .005$). Female participants more frequently preferred the male to pay with more attractive males.

Attractiveness interactions

We analysed the data with 2 mixed ANOVAs with 3 levels of image attractiveness and 3 levels of self-rated attractiveness.

Male participants: The ANOVA showed a main effect of the images' attractiveness ($F_{2,482} = 284$, $p < .0005$), with no interaction between the attractiveness of the images and the self-rated attractiveness of participants ($F_{4,482} = 1.6$, $p = .17$). This analysis also showed a between subjects effect of self-rated attractiveness ($F_{2,241} = 3.9$, $p = .022$, see Figure 6-3& Figure 6-4).

Female participants: The ANOVA showed a main effect of the images' attractiveness ($F_{2,336} = 7.9$, $p < .0005$), with no interaction between the attractiveness of the images and the self-rated attractiveness of the participants ($F_{4,336} = 1.1$, $p = .33$). This analysis also showed a between-subject effect of self-rated attractiveness ($F_{2,168} = 3.3$, $p = .038$, see Figure 6-3& Figure 6-4).

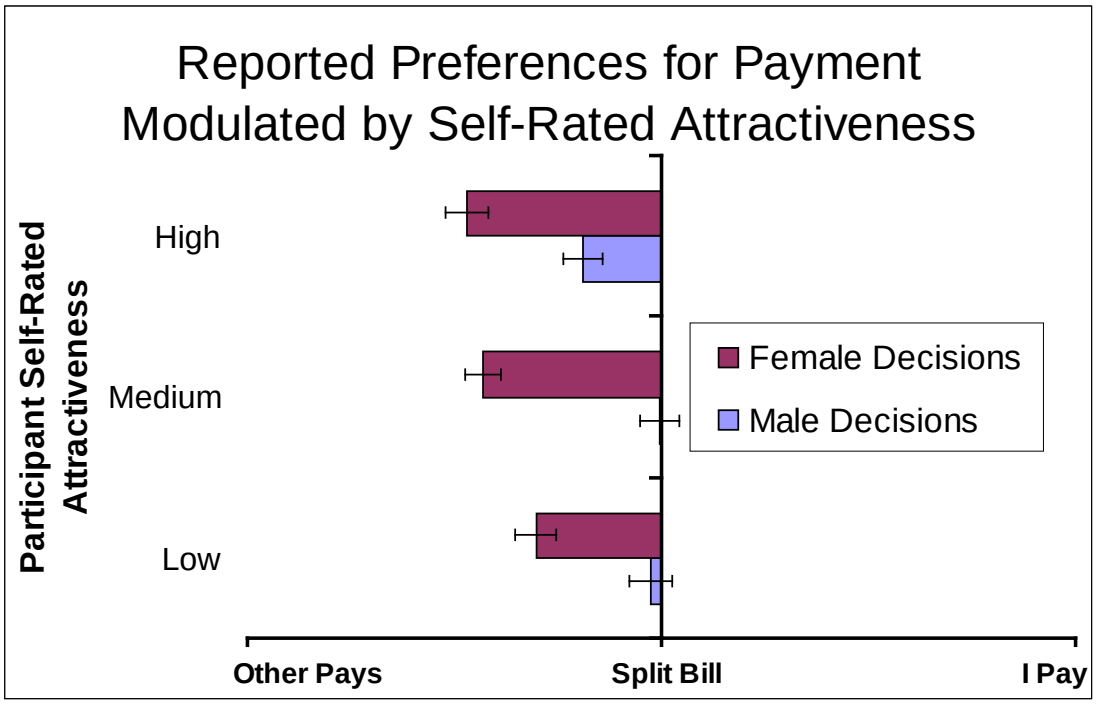


Figure 6-3 – Self-rated attractiveness predicts a shift in preference of both sexes toward the opposite sex paying for the meal. Both male and female participants are more likely to prefer the opposite sex to pay for the meal if they consider themselves to be attractive.

Our hypotheses based upon sexual selection were confirmed. We found that both female and male participants modified their preferences for the opposite sex to pay for their meal in line with their evaluation of their own attractiveness. Self-reported attractiveness (an estimate of mate-value) in both male and female participants relates positively to a preference for the other to pay for the meal.

Also, while both male and female participants modified their preferences in line with the attractiveness of the observed images they did so in the predicted directions. Male participants show more willingness to pay for more attractive compared with less attractive females whereas female participants would prefer the more attractive males to pay for them compared with less attractive males.

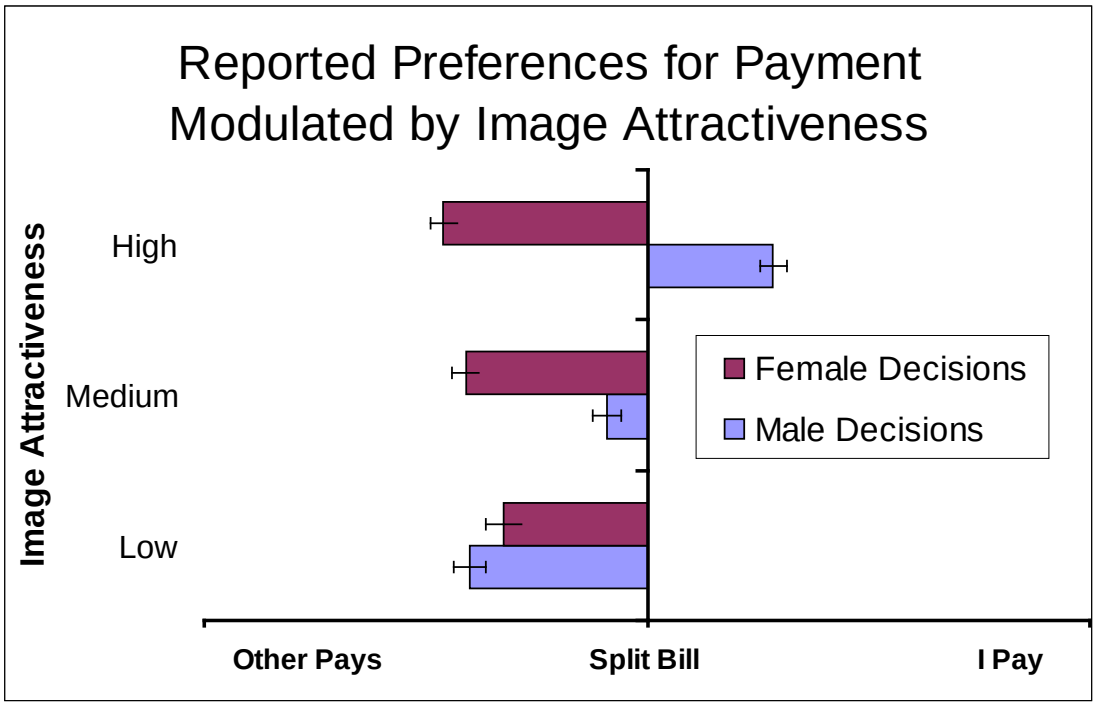


Figure 6-4 – Male participants offer to pay for attractive females; female participants prefer to be paid for by attractive males. There is a significant effect of facial attractiveness on the payment preferences of both male and female participants but in opposite directions.

Discussion: Preferences Predicted by Mating Market

In our sample, patterns of human preferences for payment in romantic dates conform to predictions derived from a mating market framework based on sexual selection theory in three ways. First, females significantly more often reported a preference for males to pay than males preferred the females to pay. Second, participants' self-rated attractiveness predicted their preference for their date to pay for the meal. Third, the attractiveness of the date had opposite effects on the reported preferences of male and female participants. Male participants were more willing to pay for more attractive dates, while female participants preferred that more attractive dates pay for them.

In other work on mate-value it is common to find data with a U or hump shaped pattern. As market value is a trade-off between various parameters there is likely to be an optimal trade at the top of the inverted U (e.g. age in Pawlowski & Dunbar,

1999). We might have expected a U-shaped distribution of female preferences in our data as females may have be willing to pay in order to gain social access to males with extreme good looks. The data, however, does not show this pattern; female preferences are linearly related to male attractiveness. It is possible that this is because we asked about preferences rather than expectations. If, rather than asking who they would prefer to pay, we had asked who participants thought would pay at the end of the meal we may have found something more like a U-shape as the particpants may want the most attractive males to show interest in them and pay but nevertheless recognise that they may end up paying themselves.

Women prefer to have their meals paid for by men in proportion to their own mate value. If payment acceptance indicates sexual interest then women with higher mate value (more attractive women) more often indicate sexual interest. While we would not want to say that an indication of sexual interest leads directly to coitus – a second date is the more likely next step – there is evidence that female self-rated attractiveness correlates with a less restricted attitude to short-term relationships (Clark, 2004) and at the same time, men rate the faces of women with more unrestricted attitudes to short-term relationships as more attractive (Boothroyd, Jones, Burt, & Perrett, 2008). Our data here would be consistent with attractive women (compared with less attractive women) actively wanting and therefore indicating their preference for short-term relationships but it would also be consistent with attractive women more often indicating that they want a second date and therefore placing themselves more often in contexts where the relationships (long or short-term) they would choose are possible.

We conjecture therefore that the commodity offered by females is social access such as the second date. If this is true then the reported preferences for payment should predict reported preferences for a second date. Women should therefore trade-off payment for the meal against facial attractiveness. This should have the effect that while women should be willing to go on a second date with the most attractive males and unwilling with the least attractive males whether they pay for the meal or not, the average attractive males are likely to get a second date if they pay and not if they don't. Investigating participant payment preferences for meals on a second date would also allow greater contrast with other explanatory mechanisms such as reciprocity. We plan to test these hypotheses in future experiments.

On the basis of the results here we would also predict that other demographic variables should effect similar results. Items such as male social or physical dominance, masculinity, prestige, socio-economic status and age should predict male self-evaluations of mate value and therefore willingness to pay for meals. As a corollary, in contradiction to expectations that as sexual economic inequality reduces so should expectations for the men to pay, if the mating market interpretation of our data is correct the socio-economic status of women should predict women's preferences to be paid for. Women with higher socio-economic status should consider themselves to have higher mate value [albeit that males consider female status a luxury rather than necessary value as mentioned above (Li, et al., 2002)] and therefore should demand more male investment; women with higher salaries should report a higher preference for men to pay for the meal than women with lower salaries (at least on the first date) and should perhaps expect that meal to be more costly. Indeed, in work by Waynforth and Dunbar (Waynforth & Dunbar, 1995)

comparing between socio-economic groups men from a wealthier group emphasise female attractiveness whereas women from a poorer group emphasise family commitment. We may therefore expect that higher status would effect stronger sex specific preferences.

In conclusion, we found that women preferred male dates to pay (especially when those dates were attractive males) and men showed a willingness to pay for female dates (especially when those dates were attractive females) and that both men and women modulated their preference in line with self-perceived mate value; Self-rated attractiveness in both sexes predicted a shift in preference toward the opposite sex paying for the meal.

These effects of attractiveness on dating preferences support the notion that payment and acceptance of payment on dates is recognised by both sexes as a display of sexual interest in a mating market. Individuals show financial choices in this mating market that are adaptive to evaluations of their own quality and that of prospective partners.

Section 2 Summary:

In Trust Games men make a display of pro-social behaviour, especially with attractive women. Women are more likely to exploit this display from attractive men and keep interactions with less attractive men on a reciprocal basis. Men also seem to show a preference to display investment strategies with attractive women in a dating context and women show an increased preference to accept this investment from more attractive men. Both men and women modulate their preferences in line with their own self-perceived mate-value; if they consider themselves to be attractive they more often prefer their date to pay for them. Trust game behaviour is modulated by inter-sexual competition.

Section 3

Competition and Sexual Selection

We present evidence for competition effects on trust and trustworthiness. All participants' behaviour is related to counterpart level of circulating testosterone. From previous chapters we saw that less dominant males (who are not necessarily less attractive) pay more attention to female attractiveness than do more dominant males when making trust decisions. More dominant males are also less reciprocating with other males; they may be able to afford to 'play the game' because they are likely to win in any aggressive interaction and therefore have less need of social alliance.

Chapter 7: Facial cues to circulating testosterone are predictive of others responses.

Chapter 8: Male variation in facial width to height ratio predicts how trustworthy males are in playing games and is also used by others as a cue whether to trust males.

Chapter 7

Testosterone and Trust Games

Abstract: Individuals with high basal testosterone tend to be more aggressive (Archer, 1991) and in economic games are more likely to punish unfair offers (Burnham, 2003). Therefore economic game players with access to facial information should be both less willing to choose to play games with higher testosterone counterparts and also less willing to play unfairly with higher testosterone counterparts. We tested this prediction in 'trust games' where participants decided whether or not to trust and to reciprocate the trust of counterparts depicted as static faces. As predicted we found participants' decisions whether or not to trust counterparts were related to counterpart's testosterone; higher testosterone counterpart faces were trusted less frequently (although this was not replicated in expt. 2). Also as predicted, participants more frequently reciprocated the trust of counterparts with high salivary testosterone than that of counterparts with lower salivary testosterone. This may indicate that players perceive cues to counterpart testosterone and avoid the possible increased costs of interaction and reactive-aggression with higher testosterone counterparts.

The main mechanism of sexual selection other than partner choosiness is direct same-sex competition. We were therefore very interested in measures of dominance and/or aggression and how these were implicated in individual differences in game play.

We saw in Chapter 4 that males who reported higher physical dominance – i.e. that they would win a physical fight with a same-sex peer – were less biased by female attractiveness in their game decisions (see Figure 4-3) and were less reciprocating with other males (see Figure 4-5) than were those males who reported a lower physical dominance. We predicted these results because more dominant males should have less need to display cooperation in order to gain female attention and would have less need to cooperate to gain resources. These two results should be separated because direct competition between males would result from intra-sexual competition whereas variation in male sexual display toward females would be a result of inter-sexual competition (and male advertising as a secondary effect).

Also as discussed in Chapter 4 similar phenomena have been seen by other researchers such as male fluctuating asymmetry predicted Ultimatum Game offers (Zaatari & Trivers, 2007) and male physical attractiveness predicted a lack of cooperation in Prisoner's Dilemma, Allocator Choice, Faith, and Trust Games (Takahashi, et al., 2006). Our presented data is supportive of the contention by Zaatari and Trivers that males in better or stronger physical condition may have "superior ability in obtaining resources, especially in situations involving aggression" (2007). The more physically able males gain less from strategic alliances with others

than do weaker males. They may be able to use aggression and coercion more easily and would therefore be less cooperative.

The hormone testosterone is implicated in increased aggression and behaviours aimed at achieving or maintaining high status (Archer, 1991; Mazur & Booth, 1998; Olweus, et al., 1980; Zitzmann & Nieschlag, 2001). Testosterone is also linked to facial characteristics in that ratings of masculinity in male faces are predicted by measure of salivary testosterone (Penton-Voak & Chen, 2004) and facial masculinity and testosterone level interact with competitive game outcomes (Pound, et al., 2009). In addition to this testosterone is related to economic game behaviour as males with higher circulating testosterone are more likely to punish unfair economic game offers than are individuals with lower circulating testosterone (Burnham, 2003).

We therefore predict that participants will allow facial cues to underlying circulating testosterone to modify their behaviour when playing economic games. We expected that the faces of higher testosterone males may elicit a differential response in trust and reciprocity from others.

We also tested for the effect with female faces. Similar effects of testosterone, or at least masculinity, are to be found in women. It is a consistent effect that men are more interested in casual sex than women (Oliver & Hyde, 1993). Mikach and Bailey (1999) compared two samples of women; one sample was taken from women who had had a typical number of lifetime sex partners (mean = 4.1) and another sample from women with a considerably greater number of lifetime sex partners (mean = 57.5) than average. They found that these groups did not differ in attractiveness,

family background or self-esteem. The women with more lifetime partners were, however, also rated as more masculine and self-described themselves as masculine and more often reported childhood behaviour as being a 'tom-boyish.' Mikach and Bailey made no testosterone measures but suggest; "both unrestricted sociosexuality and masculine gender identity and role [may be] indicators of an underlying masculinization [sic] of the brain" (p149).

Testosterone appears to be an explanatory factor for such male-typical behaviours. Testosterone is a component determining face preferences within individuals. Welling *et al* (2007) demonstrated that when making attractiveness judgements for male faces across the female cycle, females show an increase in preference for masculine male faces over feminine male faces when circulating testosterone is higher than at other points in the cycle (and other hormones are constant). A preference for more masculinity in males would be consonant with increased risk-taking and a reduced restriction in attitude to casual sex.

Physiological effects of testosterone could to some extent explain more masculine behaviours in women. Schreiner-Engel *et al*. (1981) found positive correlations between female salivary testosterone levels and genital response to erotic stimuli in the laboratory. Tuiten *et al* (1996) confirm testosterone as a mechanism for this, rather than a correlate, when they found that genital response was increased in amenorrheic women by testosterone administration. The North American Menopause Society (2005) has also found positive enhancement of sexual function in menopausal women with regard to desire, arousal, and orgasm with application of topical testosterone over that driven by placebo.

Raised testosterone in women does not only increase male-typical attitudes in women with regard to sex. Dabbs *et al* (2002) show that participants of both sexes describe feelings of increased arousal and, most noteworthy here, aggression. Participants scored more highly on implicit-attitude measures of arousal and aggression when their testosterone level is increased by application of testosterone gels to the skin when compared with a placebo. The placebo condition also showed significantly greater self-report and implicit measures of arousal and aggression than participants who ingested liquorice capsules (which lowers testosterone). The effects were stronger for women that for men. This supports the idea that just as high average basal testosterone males tend to be aggressive (Archer, 1991) high testosterone females are likely to be similarly aggressive and dominance seeking.

These reported effects of testosterone upon female physiology and behaviour support the contention that testosterone has similar effects upon females and males. It is therefore likely, although not demonstrated, that naturally occurring variation in testosterone amongst women may also affect female facial appearance in a way that allows prediction of behaviour. Given that male testosterone measures predict ultimatum game punishment for unfair behaviour (Burnham, 2003) it is likely that female circulating testosterone measures and facial correlates would also predict punishment.

Predictions with regard to the effect of testosterone on Trust Game behaviour were as follows. 1) Higher testosterone individuals are likely to be more aggressive, possibly hostile; players may avoid this interaction and decide not to trust higher testosterone individuals although not being trusted in a trust game increased

testosterone in men (Zak, Borja, Matzner, & Kurzban, 2005) which may suggest a reverse causation, that males who are not trusted, for whatever reason, have higher levels of testosterone. We, nevertheless, predict that higher testosterone faces will be trusted less than lower testosterone faces. 2) Failing to reciprocate when trusted in the reciprocation role does implicate an unfair action and higher testosterone individuals would be motivated to punish (or at least reward less) such behaviour. Although there is no opportunity to punish unfair behaviour in our game we predict that game players may operate with a heuristic that biases them against playing unfairly with higher testosterone counterparts. We predicted that participants would reciprocate trust more often with higher testosterone individuals.

Experiment 1: Testosterone and Trust (St Andrews Images)

Stage 1 – Images and Hormones

50 female and 50 male St Andrews students (white; aged 18-25) attended for the hormone assay and were also photographed.

The Hormone Assay:

Female participants attended on two to four occasions. The interval between each test session was one week. On attendance the participants were instructed to first rinse their mouths with water and then salivate passively into the containers rather than chewing a wad of cotton wool to avoid possible inflation of the testosterone levels (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004) or contamination with phytooestrogens. Participants had not eaten for at least an hour prior to testing sessions. Participants deposited between 3 and 5 mL of saliva by spitting directly into plastic pharmaceutical vials at the beginning of each testing session. The vials were

then sealed and frozen at -20°C. Although different participants were tested at different times of day each participant always attended at the same time of day.

Hormonal assays were performed by the biological sciences lab at Queen Margaret University College (Edinburgh, UK). Salivary testosterone levels were determined by the ELISA method (Al-Dujaili, 2006; Sharp & AlDujali, 2004). The assay procedure was based on the indirect, competitive binding technique with samples first extracted using diethylether (the protocol is described in Welling, et al., 2007). Mean testosterone values across the multiple testing sessions were calculated. Average testosterone for the females = 96.82 pg/ml, N=50, SD = 51.58 pg/ml. These testosterone levels are within population norms for young adult females (see also Deady, Law Smith, Sharp, & AlDujali, 2006).

Male participants attended between 1400 and 1500 hrs on more than one occasion each occasion being at least 24 hours apart. During the 5-10 minutes following arrival in the lab and experimental briefing participants were instructed in the same way as the female participants. Hormonal data were assayed in the same way as the female assays already mentioned. Mean testosterone values across the two testing sessions were calculated. Average testosterone for the whole sample = 259.73 pg/ml, N=48, SD = 56.94 pg/ml. This is within the normal range for the QMU lab.

Stage 2 – Attractiveness

Forty one participants (17 male/24 female; mean age = 21, s.d. = 3.29) rated the 100 facial images. Images were masked (to exclude hair and clothing) and presented in random order. Participants were white and aged 18–24. Each image was assessed on a likert-type scale of 1–7 for attractiveness.

Attractiveness for each facial image was calculated as the mean rating for that face across all participants. For all 41 raters the reliability of attractiveness ratings was high (Cronbach's $\alpha > 0.9$).

Stage 3 – Trust game

63 St Andrews students (14 male/49 female; mean age = 21.1, s.d. = 1.81) were recruited from an undergraduate psychology class at the University of St Andrews. These participants were recruited at least two years after those who supplied the images and hormone assays; it is therefore unlikely that participants would be familiar with their game counterparts. Participants took part in 'two-person' sequential trust games as described in chapter 1.

Participants were given written instructions on how the game was played (see Appendix 1) and a flow chart of the game was present on screen throughout (See Appendix 2). The only information available to participants about their counterpart for each game was the presented masked images (to exclude hair and clothing). The games were split into two blocks by sex of facial image and these were played in random order. Within each block the images were also presented in random order.

Each block of facial images were split randomly into two sets. 25 images were assigned to always play the counterpart to participants as player 1 and 25 images assigned to player 2. 25 filler images were also used to represent 25 counterparts who chose not to trust the participant.

Participants did not play the games for real money but instead received course credit for taking part.

Experiment 1: Results

In line with the literature participants in the trust game made decisions predicted by the attractiveness ratings of their counterpart's image. Attractiveness ratings correlate with proportion of decisions to trust ($N = 50$, $r = .54$, $p < .0005$). Also participants decisions whether or not to reciprocate with a fair proportion of the £8 as player 2 were significantly correlated with attractiveness ratings ($N = 50$, $r = .40$, $p < .001$).

It is possible that testosterone measures will interact with attractiveness, therefore it is necessary to control for attractiveness in any exploration of the results.

Male Faces:

The mean proportion of decisions to trust as player 1 was 0.46 and the mean proportion of decisions to reciprocate trust as player 2 was 0.68. This is consistent with typical responses in the trust game (Camerer & Fehr, 2004).

Analyses of the results by face with Pearson 1-tailed correlations were carried out. We found no significant relationship between salivary testosterone and proportion of decisions to trust faces ($N = 25$, $r = -0.07$, $p = .36$). Neither did we find a significant relationship between salivary testosterone and the proportion of decisions to reciprocate ($N = 25$, $r = -0.05$, $p = .40$).

Testing across all faces, testosterone measures and attractiveness ratings are not significantly correlated with each other ($N = 49$, $r = .07$, $p = .34$). The partial correlation between testosterone and proportion of trust and reciprocal response is not significant when controlling for attractiveness (Trust response; $N = 25$, $df = 22$, $r = -0.12$, $p = .28$; Reciprocation response; $N = 25$, $df = 22$, $r = -0.06$, $p = .39$).

Experiment 1
(Trust Condition):
Composite of Low Testosterone Males

Experiment 1:
(Trust Condition)
Composite of High Testosterone Males

Figure 7-1: Male faces, trust condition.

However, analyses by participant showed significant results. We grouped faces by a median split on testosterone measure into greater and less than 250 pg/ml testosterone measures. See Figure 7-1 and Figure 7-3 for visualisation of differences between groups. Participants decided to trust faces in the lower testosterone group significantly more often ($t = -3.08$, $df. = 62$, $p = .003$; see Figure 7-2) There was a significant difference in proportion of decisions to reciprocate between the high and low testosterone faces with high testosterone faces eliciting more reciprocation ($t = 3.49$, $df. = 62$, $p = .001$; see Figure 7-2). These groups are also significantly different in attractiveness but matching the groups for attractiveness by excluding the most attractive member of the high testosterone group increased the significance of the difference between low and high testosterone groups for reciprocation. This is the only pair in all experiments where difference in attractiveness could explain the

behavioural difference toward testosterone groups. There has not been time nor space to incorporate discussion of these analyses within the text.

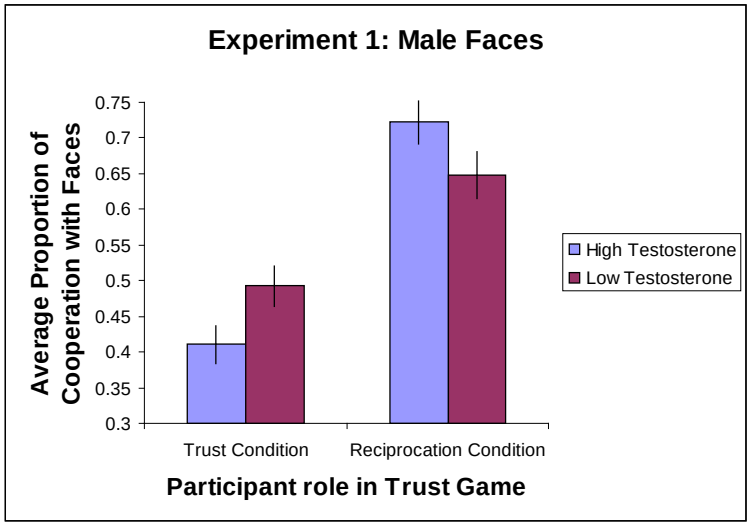
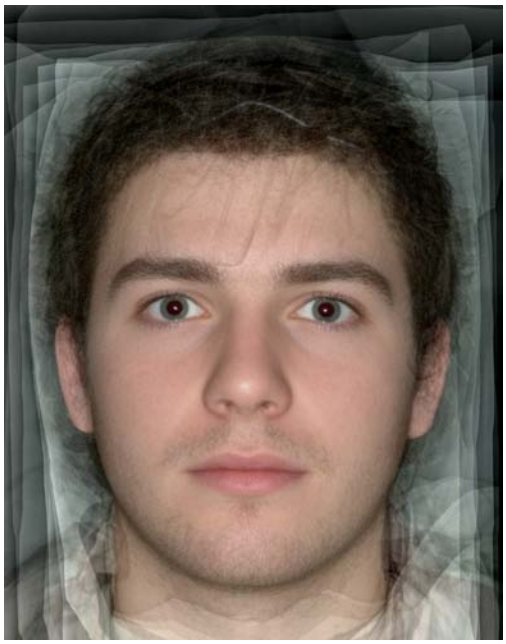


Figure 7-2 – Participants' response to lower testosterone male faces was significantly more trusting than their response to higher testosterone male faces (t = -3.08, df. = 62, p = .003) and participants reciprocated less frequently with low testosterone male faces than with high testosterone male faces (t = 3.49, df. = 62, p = .001)

Experiment 1 (Reciprocation Condition): Composite of Low Testosterone Males



Experiment 1: (Reciprocation Condition) Composite of High Testosterone Males

Figure 7-3: Male faces, reciprocation condition.

Female Faces:

The mean proportion of decisions to trust as player 1 was 0.51 and the mean proportion of decisions to reciprocate trust as player 2 was 0.66. This is consistent with typical responses in the trust game (Camerer & Fehr, 2004).

Analyses of the results by face with Pearson 1-tailed correlations were carried out. We found no significant relationship between salivary testosterone and proportion of decisions to trust ($N = 25$, $r = .03$, $p = .45$). Neither did we find a significant relationship between salivary testosterone and the proportion of decisions to reciprocate ($N = 25$, $r = .06$, $p = .39$).

Testing across all female faces, testosterone measures and attractiveness ratings are not significantly correlated with each other ($N = 50$, $r = .12$, $p = .21$). The partial correlation between testosterone and proportion of trust and reciprocal response is not significant when controlling for attractiveness (Trust response; $N = 25$, $df = 22$, $r = 0.06$, $p = .5$; Reciprocation response; $N = 25$, $df = 22$, $r = 0.11$, $p = .31$).

Experiment 1
(Trust Condition):
Composite of Low Testosterone Females

Experiment 1:
(Trust Condition)
Composite of High Testosterone Females

Figure 7-4: Female faces, trust condition.

Analyses by participant showed significant results. We grouped faces by a median split on testosterone measure into greater and less than 80 pg/ml testosterone measures. See Figure 7-4 and Figure 7-6 for visualisation of differences between groups. Participants decided to trust faces in the lower testosterone group significantly more often ($t = -4.46$, $df. = 62$, $p < .0005$; see Figure 7-5) Supporting our second hypothesis there was a significant difference in proportion of decisions to reciprocate between the high and low testosterone groups ($t = 2.09$, $df. = 62$, $p < .05$; see Figure 7-5).

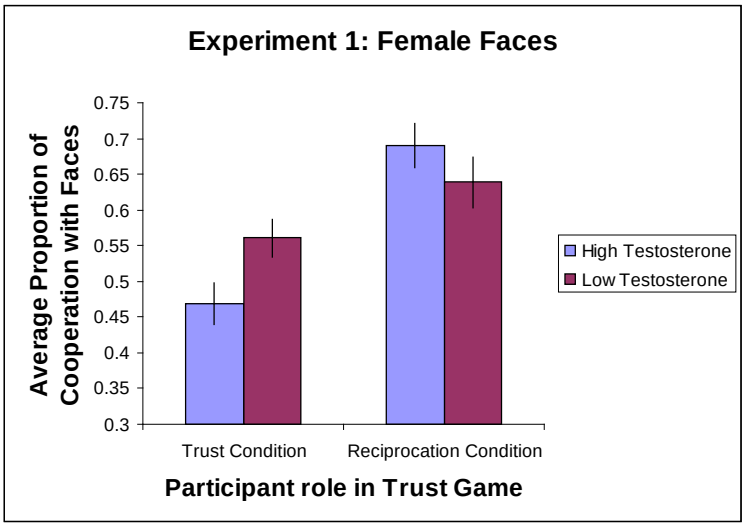


Figure 7-5 – Participants' response to lower testosterone female faces was significantly more trusting than their response to higher testosterone female faces (t = -4.46, df. = 62, p < .0005) and participants reciprocated less frequently with low testosterone female faces than with high testosterone female faces (t = 2.09, df. = 62, p = .04)

Experiment 1 (Reciprocation Condition): Composite of Low Testosterone Females

Experiment 1: (Reciprocation Condition) Composite of High Testosterone Females

Figure 7-6: Female faces, reciprocation condition.

These results clearly support our two hypotheses. Participants decide to trust lower testosterone faces of both sexes with greater frequency than they decide to trust

higher testosterone faces. Participants also decide to reciprocate trust more frequently with higher testosterone faces than with lower testosterone faces, again with both male and female faces.

Participants were only rewarded with course credit for taking part in this experiment. Therefore, in this experiment, decision making heuristics that are completely unrelated to financial consequences could have been used by participants. In experiment 2 the participants receive financial reward for the outcome of the games.

As the image set was drawn from St Andrews students it is also possible that participants may have had some experience of the individuals in the images. This is improbable as the students in the images were from previous years' participants and the protocols offered participants the option of declaring previous knowledge of individuals on screen. In experiment 2 images of students from a different university were used.

Experiment 2: Testosterone and Trust (Aberdeen Images)

Stage 1 – Images and Hormones

Participants were recruited in the Aberdeen area by means of an advertisement. Non-Caucasian faces were excluded on the basis that an 'other-race' effect might skew trust judgements. Some older participants were excluded on the basis that they were extreme outliers in age. Participants wearing make-up were also excluded. A few participants refused consent for use of their images in future studies. Fifty female participants were included.

Participants were photographed and had their circulating testosterone levels measured using a salivary assay. The photographs were rated for attractiveness.

Photography:

Participants were photographed using a digital Fujifilm Finepix S2Pro with a 60mm Nikon lens. The camera was set to 'Aperture Priority', with aperture at F16. Participants sat at a distance of 48cm from the camera. The light source was restricted to flash guns. Images were masked (to exclude hair and clothing) using Psychomorph (See Tiddeman, et al., 2001).

The Hormone Assay:

Protocols and analysis were carried out as per experiment 1.

Mean testosterone values across the multiple testing sessions were calculated. Average testosterone for the whole sample = 109.88 pg/ml, N=50, SD = 66.39 pg/ml. (Group in decision to trust condition mean = 112.67 pg/ml, N=25, SD = 69.32 pg/ml; Group in decision to reciprocate condition mean = 107.1 pg/ml, N=25, SD = 64.64 pg/ml). These testosterone levels are within population norms (see also Deady, et al., 2006).

Stage 2 – Attractiveness

Fifty three St Andrews students; 8 males (mean age = 20.75, S.D. = 0.75) and 45 females (mean age = 21.09, S.D. = 2.15) assessed each facial image for attractiveness on a likert-type scale of 1–7. The images were presented in random order. The ratings were carried out as part of a larger study. Participants rated three blocks of stimuli in a randomised order: (a) these faces for attractiveness, (b) the perceived age of these faces and (c) the perceived age of skin patches cut from the cheek area

of these images. All stimuli within the blocks were also randomised in order of presentation. Only the attractiveness ratings are used here.

Attractiveness for each facial image was calculated as the mean rating for that face across all participants. Attractiveness ratings for all 53 raters, Cronbach's $\alpha = 0.978$ (female raters n=45, $\alpha = 0.975$, male raters n=8, $\alpha = 0.884$).

Stage 3 – Trust game

Participants from experiment 1 were recalled to take part in experiment 2. Eleven participants did not return. Fifty two participants (10 male/42 female; mean age = 21.06, s.d. = 1.67) were recruited from an undergraduate psychology class at the University of St Andrews. Participants took part in a 'two-person' sequential trust game as described above.

Participants had previously played the trust game in experiment 1 and were therefore familiar with the game but were unfamiliar with the images presented in this experiment consistent with the zero-acquaintance paradigm.

Participants were given written instructions on how the game was played (see Appendix 1) and a flow chart of the game was present on screen throughout (See Appendix 2). The facial images were split into two sets of 25. One group of images was assigned to always play the counterpart to participants as player 1 and the other group assigned to play as player 2. 25 blank white filler images were also used to represent 25 counterparts who chose not to trust the participant.

Participants were instructed that unlike in the previous set of games they would be playing for real money and that the outcome of the games would be dependant on their decisions and the previous decisions of their counterparts.

The outcome of each game was decided by participants where they were player 2 and were randomised biased to previous play for games where participants trusted as player 1 (e.g. if counterpart previous reciprocated 90% there would be a 90% chance of reciprocation). Participants were paid according to the outcome of one of the games they played.

Experiment 2: Results

Upon comparing the proportion of decisions to trust by participants in experiment 1 with their decisions to trust in experiment 2 we found that participants are consistent ($t = 1.225$, df. = 51, $p = .226$). The mean proportions of decisions to reciprocate, however, differed between experiments ($t = 2.79$, df. = 51, $p = .007$). Mean reciprocation fell from 67% in experiment 1 to 60% in experiment 2.

The mean proportion of decisions to trust as player 1 was 0.45 and the mean proportion of decisions to reciprocate trust as player 2 was 0.60.

Participants made decisions predicted by the attractiveness ratings of their counterpart's image. Attractiveness ratings correlate with the average proportion of decisions to trust ($N = 25$, $r = .66$, $p < .0005$; see Table 7-1). Also the average of participants' decisions whether or not to return a fair proportion of the £8 as player 2 were significantly correlated with attractiveness ratings ($N = 25$, $r = .54$ $p = .006$; see Table 7-1).

Like experiment 1 we found participants' decisions whether or not to trust counterparts were unrelated to their counterpart's testosterone level ($N = 25$, $r = .22$, $p = .14$). Unlike experiment 1, however, the average participants' proportion of

decisions to reciprocate with their counterparts positively correlated with the salivary testosterone of their counterparts and participants returned £4 rather than £2 more often to individuals with higher testosterone assays (N = 25, r = .47 p = .019; see Table 7-1).

	Decision to Trust	Decision to Reciprocate
Attractiveness	r = 0.66, p < .000	r = 0.54, p < .01
Testosterone	r = 0.22, p = .285	r = 0.47, p = .019

Table 7-1 - Participants place more trust in more attractive faces. Participants returned significantly more to more attractive and higher testosterone faces.

As it is possible that higher testosterone females are also higher in attractiveness we checked whether this was a spurious result with partial correlations.

Partialling out attractiveness the correlation between testosterone and proportion of reciprocation was significant (N = 25, df = 22, r = .57 p = .004). The effect of attractiveness was significant when testosterone measures were controlled (n = 25, df = 22 r = .62 p = .001). Testosterone and attractiveness ratings did not correlate (n = 50, r = .03, p = .825).

Comparison by participant also showed significant results. Grouping faces by a median split on testosterone measure into greater and less than 106 pg/ml testosterone and comparing the mean reciprocation response by participant there was a significantly higher level of reciprocation toward high testosterone faces (t = -4.96, df. = 51, p < .0005; see Figure 7-8). This is further support of our hypothesis that higher testosterone predicts higher reciprocation from others in trust games. See Figure 7-9 for visualisation of differences between groups.

Experiment 2
(Trust Condition):
Composite of Low Testosterone Females

Experiment 2:
(Trust Condition)
Composite of High Testosterone Females

Figure 7-7: Female faces, trust condition.

Testing by participants on a median split on testosterone of the images in the trust condition found no significance. Participants did not decide to trust lower testosterone faces more frequently than higher testosterone faces (t = -1.255, df. = 51, p = .215; see Figure 7-8). See Figure 7-7 for visualisation of differences between groups.

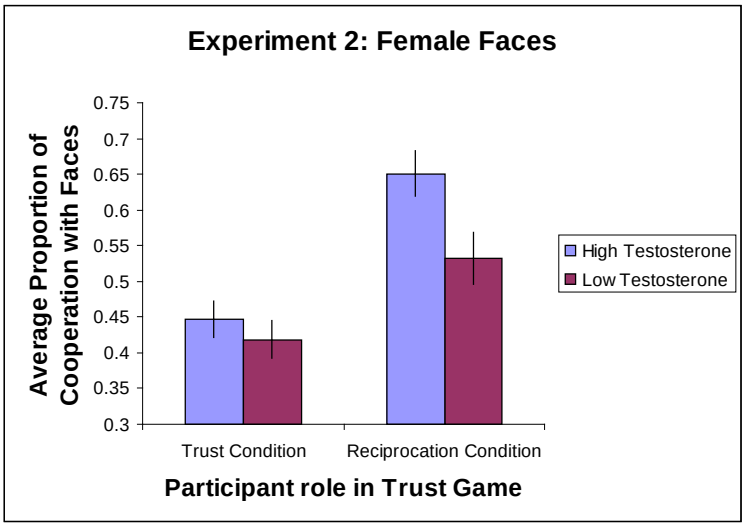


Figure 7-8 – Participants showed no significant difference in trust toward high vs. low testosterone faces. However, response to higher testosterone faces was significantly more reciprocating than their response to lower testosterone faces. (t = -4.96, df. = 51, p < .0005)

Experiment 2
(Reciprocation Condition):
Composite of Low Testosterone Females

Experiment 2:
(Reciprocation Condition)
Composite of High Testosterone Females

Figure 7-9: Female faces, reciprocation condition.

Discussion

In this study we replicate the findings of others that attractiveness is a determinant of both decisions to trust (Mulford, et al., 1998; Solnick & Schweitzer, 1999) and decisions to reciprocate trust (Wilson & Eckel, 2006).

We hypothesised that testosterone should also be a determinant of these decisions. We find as predicted, that lower testosterone faces are more trusted by participants than are higher testosterone faces. This was a very strong effect in both the female and male faces of our first experiment. A possible reason for this not being wholly replicated in the second experiment is that as the second experiment was played with real money. Participants playing for real money in experiment 2 reciprocated less. With regard to trust decisions there is a motivation to mistrust those we think untrustworthy and therefore not trust the high testosterone face (as in experiment 1) but where the game has real financial consequences (as in experiment 2) lack of trust in the second player has financial consequences and prevents the second player from earning an extra pound and could be construed as negative behaviour. In experiment 2 there may be reason to mistrust high testosterone individuals at the same time as reason to avoid punishment from them. This may explain the lack of a significant result.

In both experiments, as predicted, we find that higher testosterone faces elicit a greater proportion of reciprocal responses than do lower testosterone faces.

In the second role of the trust game the simple self-interested strategy is to always take the unfair proportion, in other words to never reciprocate. The participants do not know their counterparts and have no real reason to suppose that they will ever meet them subsequent to the games. However despite this, participants forgo the extra money available to them in order to play the game somewhat fairly. This is typical of participant behaviour in these games (Camerer & Fehr, 2004). The fact that level of counterpart's testosterone predicts how likely participants are to reciprocate

combined with previously published results that testosterone predicts frequency of punishment (Burnham, 2003) seems to indicate that participants are operating with some expectation of further interaction and are avoiding punishment.

Punishment may indeed be overt retribution for unfair behaviour but could also take the form of indirect social cost, perhaps the loss of ongoing social acceptance. Paunonen (2006) found that manipulations in descriptions of honesty associated with facial images would predict subsequent ratings for attractiveness, health, kindness and femininity. *A forteriori*, experience of actual unfair behaviour is likely to make counterparts rate participants as less attractive, healthy and kind. In other words, behaving in an unfair way may lead to later social exclusion or indeed physical punishment. Participants seem to behave with the heuristic that this matters more with higher testosterone counterparts.

A weakness of our experiments here is the preponderance of female images and female participants. We would argue as we have above that testosterone should have similar behavioural effects in women as in men but these experiments would gain considerably from replication with male participants and images. We would predict that effects would be stronger in male – male interactions.

Discussion: Testosterone Cues Less Trust but More Reciprocation

Current circulating testosterone level modulates decisions in Trust Games. Male and female counterparts with higher testosterone level are less trusted and elicit greater reciprocation. An exception to this in our data was seen in experiment 2 where testosterone level showed no relationship with trust decisions. This may be due also

to players being wary of behaving uncooperatively with counterparts who had a raised testosterone level.

All our results here may be explained as participants avoiding perceived reactive-aggressive interactions.

Chapter 8

Male Facial Width and Trustworthiness

The following report (Previously published as Stirrat & Perrett, 2010) demonstrates further evidence of direct competition between males which influences decisions in Trust Games by exploring the relationship between Trust Game behaviour and a facial measure that has been shown to relate to male dominance and reactive-aggression. The more physically robust males, those with high facial width to height ratios, are less trustworthy and moreover are seen as less trustworthy. It is reasonable to suppose that these more robust males are more likely to be more competent in agonistic interactions.

M. Stirrat and D.I. Perrett. Valid facial cues to cooperation and trust: Male facial width and trustworthiness. *Psychological Science* 21(3) 349-354 (2010)

Abstract: Decisions about whom to trust are biased by stable facial traits such as attractiveness, similarity to kin and perceived trustworthiness. Research addressing the validity of facial trustworthiness or its basis in facial features is scarce and has inconsistent results. We measured male trustworthiness operationally in Trust Games where participants had options to collaborate for mutual financial gain or exploit for greater personal gain. We also measured facial (bizygomatic) width (scaled for face height) as this is a sexually dimorphic, testosterone-linked trait predictive of male aggression. We found that men with greater facial width were more likely to exploit the trust of others and that other players were less likely to trust male counterparts with wide rather than narrow faces (independent of their attractiveness). Moreover, manipulating this facial width ratio with computer graphics controlled attributions of trustworthiness, particularly for subordinate female evaluators.

The human face is perhaps the most salient source of interpersonal information, especially with strangers. We can judge extroversion and conscientiousness accurately from the face slightly above chance (Penton-Voak, et al., 2006). There is consensus in perceptions of facial trustworthiness (Zebrowitz, et al., 1996) but evidence for validity in these judgements is patchy.

Decisions about whom we trust are biased by stable facial traits such as attractiveness (Wilson & Eckel, 2006), similarity to kin (Debruine, 2002) and perceived trustworthiness (van 't Wout & Sanfey, 2008). There is some evidence that people can judge from a face whether someone would be at ease with deception (Berry, 1990; Bond, et al., 1994) although others have failed to replicate this result (Masip & Garrido, 2001) and have found either no correlation or a negative correlation between judgements of faces and objective measures of trustworthiness (Hassin & Trope, 2000; Zebrowitz, et al., 1996). Whereas transient expressions can support accurate evaluation of non-cooperation (Verplaetse, et al., 2007), and perceptions of trustworthiness seem to relate to facial expression (Oosterhof & Todorov, 2009) there is little evidence that biases based on stable facial traits are valid.

There is evidence against the validity of judgements of facial trustworthiness. While attractive faces are trusted (Wilson & Eckel, 2006) male attractiveness (Takahashi, et al., 2006) and male symmetry (Zaatari & Trivers, 2007) predict less cooperative behaviour in economic games. Explanations for these facts have been put forward in terms of sexual selection for male dominance and sexual dimorphism.

Recently, a relationship has been found between male dominance, reactive-aggression and variation in a facial metric. Weston, Friday and Lio (2007) have shown that human adults are sexually dimorphic in skull bizygomatic width corrected for upper facial height. Variation in human male bone growth, specifically cranial growth, is related to testosterone effects in adolescence (Verdonck, Gaethofs, Carels, & de Zegher, 1999). Carré and McCormick (2008) found that variation in facial width ratio predicted male participants' other-rated dominance, reactive-aggression in the lab and number of ice hockey penalties.

Reactive-aggression in Carré and McCormick (2008) was measured as the amount of times a participant punished counterparts for stealing their points in a point subtraction task. As such, this is a measure of a pro-social behaviour that has been called altruistic punishment (see Fehr & Gachter, 2002 for discussion). We reasoned that the ability to punish may be based in greater physical robustness or dominance which would reduce consequences from agonistic interactions. Such status may also lead to increased anti-social behaviour and reduced cooperation similar to that seen by Zaatari and Trivers (2007).

We were therefore interested to explore whether male variation in facial width ratio relates to a) cooperation in economic games (experiment 1) and b) trust judgements of others (experiments 2 and 3).

Experiment 1 – Male Trust and Reciprocation

Participants

One hundred and forty-three white heterosexual University of St Andrews students participated (107 female; mean age = 21.6, s.d. = 2.3, range = 18-35).

Stimuli

A different set of fifty male and fifty female white University of St Andrews students (aged 18-25) were photographed in neutral pose one year before the current experiment.

Procedure: Trust game

Participants were informed that they would play a series of economic games for real money. They then gave consent, completed demographic questionnaires and were photographed. Participants were informed that the outcomes of their games would be dependent upon their decisions and the previous behaviour of their counterparts. We used a binary choice version of the Trust Game (Berg, et al., 1995; Huck, et al., 2007).

Participants played 49 games with male counterpart images and 50 games with female counterpart images. For each game the only information available about counterparts was a facial image masked to exclude hair and clothing. Images were split by sex into two blocks of games, counterbalanced in order of presentation and within each block images were randomly allocated for participants to make either the first or second move.

The first mover chose between ending the game (each player gets £3) or entrusting money to their counterpart. If the first mover trusted the second then £2 is added and the second mover decided to either split the money fairly (each player gets £4) or unfairly (first mover gets £2, second mover gets £6). The first move is therefore an operational measure of trust and the second a measure of trustworthiness.

Before the games started participants ran through examples of possible games and possible pay-offs to familiarise them with possible outcomes. Participants reported counterparts they recognised. These trials were omitted from analysis.

Participants were paid at an exchange rate of £1 for every £100 earned (earnings ranged from £3 to £6).

Facial Measure

Following the methodology of Carré and McCormick (2008) we measured and calculated the ratio of bizygomatic width to upper face height of participants from their photographs (see Figure 8-1).

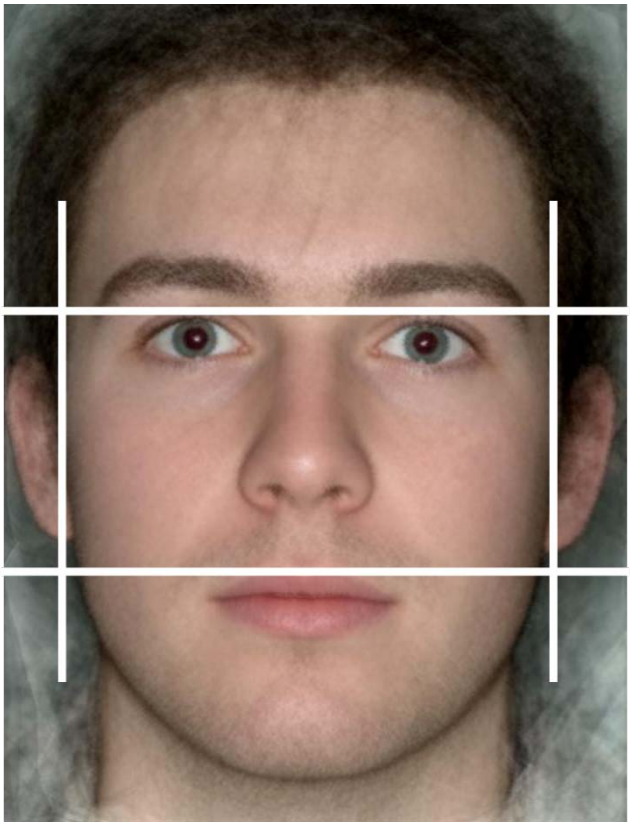


Figure 8-1 – Bizygomatic width and upper face height calculated from 2-D images. All measured images were aligned and scaled to the same horizontally level eye points. Bizygomatic width was calculated as the maximum horizontal distance from left facial boundary to right facial boundary. Upper face height was calculated as the vertical distance from the higher point of the upper lip to the highest point of the eyelids. Facial width ratio was calculated as width/height.

Analysis

Participants' play was summarised as the proportion of decisions to trust and the proportion of decisions to reciprocate with male images, female images and all images. Spearman correlations were calculated to test for a relationship between participant facial width ratio, trust and reciprocation.

Results and Discussion

Females, on average, trusted 45% and reciprocated with 69% of their counterparts. Female participant facial width ratio did not correlate with any of their Trust Game behaviour (see Table 8-1).

Male participants trusted 51% of counterparts and reciprocated with 72% on average. Male participants' facial width ratio showed no relation to trust decisions but did relate to decisions to reciprocate (r_s = -0.4, N = 36, p = .015, p_{rep} = 0.94: Table 8-1) – see online supplement for alternative analysis.

Male participants with higher facial width ratio (wide faces) were more likely to exploit their counterparts' trust than were males with lower facial width (slim faces).

Table 8-1 - Correlations between participant facial width ratio and Trust Game behaviour.

		All Images		Male Images		Female Images	
		r_s	p	r_s	p	r_s	P
Male Players (n=36)	Trust	-0.25	0.14	-0.24	0.15	-0.19	0.26
	Reciprocation	-0.40	**0.015**	-0.34	**0.04**	-0.41	**0.013**
Female Players (n=107)	Trust	0.13	0.17	0.09	0.35	0.13	0.16
	Reciprocation	0.16	0.10	0.10	0.29	0.15	0.11

In experiment 2 we tested whether participants' judgements of trustworthiness related to variation in male facial width ratio.

Experiment 2 – Perceived Trustworthiness

Participants

Sixty-two University of St Andrews students participated (17 males; mean age = 20.32, s.d. = 1.5).

Stimuli

We presented images of 67 white male University of St Andrews students (mean age = 20.8, s.d. = 2.7) who attended at least 2 years prior to the participant cohort and were therefore unknown to participants. These images had been previously rated for attractiveness by 41 raters (17 males: mean age = 21). Facial width ratio measures followed experiment 1 (see Figure 8-1).

Procedure: Trust game

Trust Games were conducted as experiment 1 except that participants were assigned to play only as first mover for 67 games with male counterpart images presented in random order.

Analysis

We calculated the proportion of participants that trusted each image.

We tested for normality using Kolmogorov-Smirnoff. Trust ($p > 0.2$, $p_{rep} < 0.72$), attractiveness ($p = 0.07$, $p_{rep} = 0.85$) and facial width ratio ($p > 0.2$, $p_{rep} < 0.72$) were all normally distributed.

Results and Discussion

Images were trusted by 46% (sd. = 0.21) of participants on average. Decisions were consistent across participants (Cronbach's alpha = 0.88).

A least-squares regression analysis revealed that facial width ratio predicts 16% of the variation in trust decisions (B = -3.96, d.f. = 66, R^2 = 0.157, p = .001, p_{rep} = 0.99; see Figure 8-2) with wider faces trusted less.

Image attractiveness negatively correlated with facial width ratio (R = -0.32, p < 0.01, p_{rep} = 0.96) and positively correlated with trust decisions (R = 0.54, p < 0.0005, p_{rep} = 0.99). Including image attractiveness in a regression analysis revealed that attractiveness (~30%) and facial width ratio (~6%) independently explain variance in trust decisions (Model: R^2 = 0.351, p < .0005, p_{rep} = 0.99, image attractiveness: B = 4.65, p < .0005, p_{rep} = 0.99; facial width ratio: B = -2.48, p = .023, p_{rep} = 0.92).

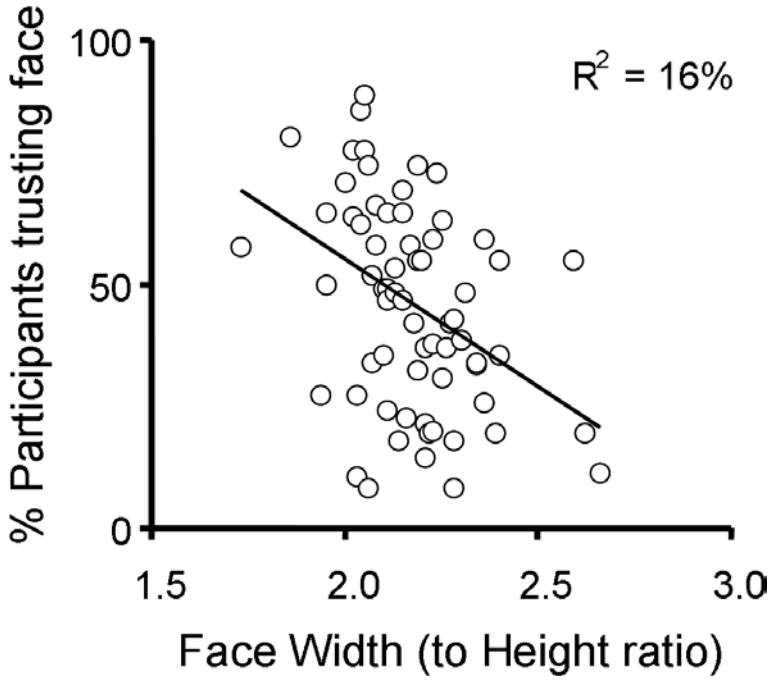


Figure 8-2 – Male facial width ratio predicts the proportion of participants that trust images.

It is clear that male facial width ratio is a cue to male trustworthiness and that it predicts trust placed in male faces. What isn't clear is that this ratio is driving trust

judgements because although we have excluded attractiveness as a correlate in our analysis it is possible that facial width ratio correlates with other facial cues. In experiment 3 we examined the effect of manipulating the facial width ratio of images on decisions to trust when other dimensions are held constant.

Experiment 3 – Manipulation of Facial Images

Participants

Two hundred and eighty-six online participants (209 female; mean age = 23.2, s.d. 4.4, range 18 - 35 years).

Stimuli

Using 3 different male image sets (n = 19; n = 36; n = 49; age range 18-27) collected at different times from different cohorts of students we made 3 prototypes of high and 3 of low facial width ratio faces to allow 3 facial width ratio transforms.

Twelve male images were manipulated; each image was a composite of 3 facial photographs to mask identity for use in online experiments. These images were manipulated in shape (Rowland & Perrett, 1995) 25% up and 25% down (see Figure 8-3) on each of the 3 facial width ratio transforms generating 3 pairs of images from each of the original 12 images

The distribution of facial width ratio of the final 72 transformed images (12 base images x 3 transforms x 2 directions) did not differ from the facial width ratio distribution of the original image sets.

Figure 8-3 – Example of high ratio (right) and low ratio (left) transformed image.

Procedure

Participants were informed that they would be viewing multiple pairs of images and that they would be asked to a) decide which of each pair looked more trustworthy and b) complete a short questionnaire. Participants gave consent.

Participants were randomly split into 3 groups and were presented with all 12 identity pairs. Presentation of images was counterbalanced such that each participant saw all 12 identities using all 3 transforms; each participant group saw different identities matched with different transforms. The order of presentation of the 12 pairs of images was randomised as was whether the high or low manipulation of each pair was on the left or right side of the screen.

Participants were given a forced choice to indicate which image of each pair looked more trustworthy.

Participants completed a short questionnaire including self-rated attractiveness and self-rated social dominance (from Puts, et al., 2006) on seven point Likert-type scales.

Analysis

For each participant the proportion of trust for high or low manipulations was calculated. There was no significant difference in decisions between the three participant groups in their mean responses (Kruskal-Wallis: df = 2, p = .95, p_{rep} = 0.12), nor were there significant differences between participant mean responses to the 3 different manipulations (Friedman: N = 285, df = 2, p = .22, p_{rep} = 0.70). There was no significant difference in mean responses between male and female participants (Mann-Whitney: $U_{208,77}$ = 8004.5, p = .99, p_{rep} = 0.04). We therefore pooled data across participant sex and groups and tested for a directional effect of image manipulation by chi-squared.

Males and females differed in age (Mann-Whitney: $U_{208,77}$ = 6315.5, p = .005, p_{rep} = 0.97) and dominance (Mann-Whitney: $U_{208,77}$ = 6316, p = .039, p_{rep} = 0.89) and were therefore split to test for correlations between trustworthiness judgements and other variables.

Results and Discussion

There were 120 participants who showed no bias or who more often chose the higher ratio image as more trustworthy and 165 participants who chose the lower ratio images as more trustworthy. Participants were significantly more likely to choose the lower ratio images as trustworthy (χ^2 = 7.11, d.f. = 1, p < .005, p_{rep} = 0.97).

There were no significant correlations between male average choices and age, self-rated dominance or self rated-attractiveness (all $p > 0.61$, $p_{rep} < 0.43$). There was, however, a significant negative correlation between female average choice of the low ratio and self-rated dominance ($r_s = -0.17$, $p = 0.018$, $p_{rep} = 0.93$). There was no relationship between female trustworthiness judgements and self-rated attractiveness ($p = 0.98$, $p_{rep} = 0.07$) or age ($p = 0.47$, $p_{rep} = 0.52$).

Male facial width ratio drives perceptions of trustworthiness especially for less dominant female evaluators. This result validated our interpretation of experiments 2.

Subordinate females may be more vulnerable to exploitative males and therefore pay more attention to their attributes in line with their interaction outcome dependency (Erber & Fiske, 1984).

General Discussion

Experiment 1 showed that the ratio of facial (bizygomatic) width to height predicts male reciprocation behaviour in Trust Games such that wider faced males are more likely to exploit trust than are slimmer faced males. In experiment 2 participants were less likely to trust male counterparts with wide rather than slim faces (independent of their attractiveness). Moreover, in experiment 3 manipulating face width with computer graphics controlled attributions of trustworthiness, particularly for subordinate female evaluators.

These results clearly demonstrate that facial width to height ratio is used as a valid cue to trustworthiness. It is less clear how this cue has originated and is maintained.

Overgeneralization of emotion perception such that the similarity of an individual's neutral expression to standard expressions such as anger or happiness may guide decisions whether to trust individuals (Montepare & Dobish, 2003; Oosterhof & Todorov, 2008). This would explain our results if a) higher facial width ratio males look angrier than lower ratio males and b) males with angry looking faces are disposed to greater exploitation of trust. Both of these hypotheses remain to be tested.

Weston et al (2007) suggest that the sexual dimorphism in facial width ratio has resulted from sexual selection "operating mainly through mate choice." Here females would have to favour wide faced males for reproduction. Explanations put forward explaining why male attractiveness (Takahashi, et al., 2006) and symmetry (Zaatari & Trivers, 2007) are negatively correlated with cooperation in economic games similarly derive from sexual selection. Better quality males need put on less cooperative display in order to attract female attention. Our data, however, shows that wide faced males are neither attractive nor trusted and are therefore inconsistent with female choice for wider faced males – although our experiments do not address mate choice directly.

A second explanation put forward by Zaatari and Trivers (2007) for attractive, symmetric men being non-cooperative is that males with "superior ability…in situations involving aggression" should be less cooperative. This interpretation fits better with our data. Physical strength and fighting ability are apparent in male faces (Sell et al., 2009) and male facial width ratio has been suggested as a possible honest signal to dominance in male-male competition as it correlates with ratings of

propensity to reactive-aggression (Carré, McCormick, & Mondloch, In Press). While reactive-aggression (altruistic punishment in the point subtraction task) is pro-social we would interpret the validity of participant perceptions of anti-social untrustworthiness to derive from the same characteristic i.e. a robust physical build. Men with 'robust' wide faces may be able to both pro-socially punish and to anti-socially exploit with relative impunity. The propensity to exploitative behaviour seen in our data appears to have created a generalized somewhat valid stereotypic association of wide facial structure with untrustworthiness.

Finally, and contrary to Weston et al (2007) who argue that facial width ratio sexual dimorphism in skull shape may have been sexually selected by female choice in the hominid line, the data here suggests that female choice (indeed, partner choice in social contexts by both sexes) if it has had any effect in this aspect of human evolution has selected against, rather than for, this sexual dimorphism while variation may have been maintained through intra-sexual selection and competitive display between males. The decrease in sexual dimorphism and reduction of physical robustness accompanying hominid evolution may have facilitated the cooperation and trust that a functional human society demands.

Section 3 Summary

The existence of male-male competition effects in the Trust Game is evidenced in the following three ways: 1) Males that consider themselves to be physically dominant are more exploitative of other males. 2) The mean level of circulating testosterone in individuals predicts others responses (to both male and female images) such that facial cues associated with high testosterone elicit reduced trust but increased reciprocation from counterparts. 3) More aggressive and physically more robust males (as measured by facial width to height ratio) are more exploitative of trust and are seen as less trustworthy. We therefore conclude that Trust Game behaviour is modulated by intra-sexual competition.

Chapter 9

Conclusion

Game theory predicts cooperation in a variety of context because various games have payoffs that are better for cooperative behaviour. If the context is best described as a Prisoner's Dilemma then cooperative strategies will not survive for long but there are many situations that organisms find themselves in which are very different from this game and in which cooperation is the norm. Human behaviour is extremely cooperative and therefore the games we play are likely to be ones where it pays the individual to be cooperative, this thesis is an examination of one area of evolutionary thinking that suggests some explanations.

Consideration of human behaviour from the point of view of evolution is not useful if our conclusions are merely post-hoc rationalisations or 'just so' stories. It has been cogently argued that the value of considering the relationship between human evolution and human behaviour is where it generates testable hypotheses about behaviour (Debruine, 2009).

With regard to human altruism and trustworthiness the possible evolutionary sources are various. Game theory from the point of view of the genes allows kin selective thinking as it is likely that any organism that pays attention to and favours positive payoffs to others that share their genes will be an organism that will be replicated. This is therefore one source of cooperation and pursuing kin selective thinking has produced findings that self-similar looking human faces bias cooperative interactions. Participants favour those that look like themselves, or in other words, that look like kin but at the same time these participants do not find the self-similar opposite sex facial images to be more attractive (Debruine, 2002; Krupp, et al., 2008)

although same-sex faces may be more attractive if they are self-similar (Debruine, 2004).

The research presented in this thesis follows a similar logic and relates to another evolutionary source of cooperation, the requirement to reciprocate over successful reproduction; sexual selection. Organisms that have game payoff preferences such that their behaviour leads to offspring with better genes or resources are also organisms that will reproduce. Sexual selective thinking allowed the generation of hypotheses with regard to aspects of face perception, particularly attractiveness, in trusting and cooperative contexts.

Sexual selection where reciprocity is required for successful reproduction leads to a mating market with a) inter-sexual competition; partner choice mechanisms (particularly female choice) leading to advertising behaviour (costly signalling) and b) intra-sexual competition (particularly male-male competition) but also to coercive behaviour or force aimed at altering market forces.

With regard to partner choice we predicted that individual preferences in economic games would be to prefer interaction with facially attractive individuals; that males should advertise cooperation, particularly to attractive females, and that females should be attentive to these displays. We also predicted that individuals should evaluate their worth in the mating market and adapt their preferences accordingly.

We saw the effect in Chapter 3 that while facial attractiveness is perceived as trustworthy (the 'halo' effect), female facial femininity (an attractive attribute related to sexual health) was trusted in excess of perceived trustworthiness. This result was followed up in Chapter 4 with evidence that males respond differently to

female than to male attractiveness such that they trust and reciprocate more with attractive females (over and above the attractiveness 'halo') and that this interacts with their self-report of whether they would win a physical fight with a same-sex peer i.e. their physical dominance such that less dominant males are more affected by female attractiveness. We interpreted this as male sexual advertising of altruism modulated by their own self-evaluation whereby more dominant males have less need to advertise in order to gain female attention.

In Chapter 5 we reported that female participants also appear to respond to male behaviour as sexual advertising. While females show trust in line with the attractiveness ('halo') of their counterparts and reciprocate more with attractive female counterparts their reciprocation responses to male counterparts are negatively related to male attractiveness. This appears to be a reciprocal signal to the male display such that females keep their interaction with unattractive males on a reciprocal basis but exploit the 'trust' of (or accept the investment of) attractive males. This interpretation might be illustrated by a woman in a bar accepting a drink from an attractive man in exchange for a few minutes of conversation compared with rejecting the offer from an unattractive man and signalling lack of interest. We supported this interpretation with hypothetical dating preferences in Chapter 6 where participants reported preferences exactly in line with mating market predictions. The results supported a mating market interpretation of the data as individuals of both sexes reported stronger preferences for the other to pay if they considered themselves to be more attractive i.e. rated themselves as high value in a mating market. Females, however, showed a stronger preference for males to pay for a meal than did males for females to pay. Also, while males were more likely to

prefer to pay if the female counterpart images were attractive, female participants showed even stronger preferences for the other to pay if the male image was attractive indicating that for these female participants accepting his payment would be a signal of interest in ongoing interaction.

Our hypotheses that trust game behaviour is modulated by inter-sexual competition mechanisms were therefore supported. 1) Attractive individuals elicit more cooperation. 2) Male participants display trust and reciprocation toward attractive female counterparts in excess of perceived trustworthiness. 3) Female participants appear to respond to male trust as a signal of sexual interest and are therefore more likely to exploit the trust of attractive males. 4) In explicitly dating contexts females are more likely to prefer attractive males to pay for the meal.

With regard to intra-sexual competition, we expected that amount of circulating testosterone would be relevant to male game play. We reported in Chapter 7 that male and female behaviour is related to the amount of circulating testosterone in their counterparts. Less trust and greater reciprocation is elicited by facial images of counterparts of both sexes with higher amounts of circulating testosterone (compared with lower), suggesting that level of aggression has a non-sex specific effect on cooperation. This effect is relevant to intra-sexual competition and the ability to acquire and hold on to resources but would also seem to be a general effect in both sexes and therefore may be indirectly relevant to sexual selection.

As already mentioned, in Chapter 4 we reported that males who considered themselves to be more physically dominant were less affected by female attractiveness when making trust game decisions. This is indicative that males

evaluate their own mating market worth in contrast with their competition but is not clearly intra-sexual competition. In that chapter, however, we also reported an effect of male-male competition such that more physically dominant males were also more exploitative of other males than were less physically dominant males.

In our final empirical report in Chapter 8 we discussed evidence for male signalling of physical dominance in the form of facial-width-to-height-ratio. This is a sexually dimorphic trait that relates to self-reports of dominance in males and is a cue to reactive-aggression (Carré & McCormick, 2008) and may be an honest signal of dominance or aggression similar to traits seen in other species such as antler size in roe deer (Vanpé et al., 2007). This cue did indeed relate to game play decisions and as reported in Chapter 8 was associated with untrustworthiness while it elicited less trust from others. We would conclude from this that males with higher facial width-to-height ratio have, or have learned to have "superior ability in obtaining resources, especially in situations involving aggression" (Zaatari & Trivers, 2007) and therefore use this competence rather than cooperation.

Our hypotheses that trust game behaviour is modulated by intra-sexual selection mechanisms of direct competition were therefore somewhat supported. 1) Male participants reporting an ability to win fights with same-sex peers are more exploitative of other males. 2) Cues to testosterone in counterpart's faces are less trusted but elicit more reciprocation. 3) The male sexually dimorphic trait facial width-to-height ratio is related to self-report of physical dominance and to increased proportion of decisions to exploit others in the trust game while also being used by others as a cue to untrustworthiness.

There is, of course, a question of how these results generalise to other populations and the world at large. First the population sample is restricted. Second, there are issues with regard to framing that have not been addressed.

The population sample has of necessity been restricted to the University of St Andrews and would therefore benefit considerable from replication at other sites. Chapter 7 in particular suffered from this problem as these experiments would be most convincingly be conducted with a large sample of male participants; this was unavailable in St Andrews.

There are also issues with the framing of the experiments which have been hardly touched here. There are very many parameters of framing that can influence behaviour, such as whether a problem is described in terms of loss or gain (Tversky & Kahneman, 1986). More relevantly here, participants' beliefs with regard to how real the games are can bias behaviour. While original experiments in the area of behavioural economics were consistently run with hypothetical situations (Kahneman & Tversky, 1979) and have since been shown to be consistent with real game behaviour it has also been shown that whether this is the case is sensitive to the exact structure and framing of games. For example while Gillis and Hettler (2007) report that participants in public goods games show the same behaviour whether it is played hypothetically or for real, in ultimatum games participant behaviour differs between these contexts. It is therefore an empirical question whether the results presented here, and particularly in Chapter 7, are due to similar framing effects. There may be framing effects throughout the experiments presented here which due to time and space have been left unaddressed.

With these provisos, we conclude that trusting and trustworthy behaviour in both sexes is biased by mating market considerations predicted by intra- and inter-sexual selection.

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Appendix 1

Experiment Instructions 1:

“You and your partner start this game with £3 each. If you co-operate with each other and pool your resources (imagine a business enterprise) you can produce an extra £2. There is a catch though, only player 2 knows how to get the extra £2 and so player 1 needs to loan all their money to get the advantage.

“The game has two stages. In the first stage player 1 chooses whether to trust player 2 with the loan (the blue boxes in fig1) or to walk away (the green boxes).

“If player 1 chooses not to trust player 2 both get what they started with i.e. £3 each.

“If player 1 chooses to trust then player 2 decides whether to run off with most of the cash or to distribute the gains evenly (blue or red boxes).

“You will play this game a number of times. You will alternate between playing player 1 and player 2. You must decide whether to trust the individual you are playing with or whether to be trustworthy with them.”

Experiment Instructions 2:

“You will play a number of games. In each of these games it is possible to earn between £2 to £4. Unfortunately, we will not be able to pay you for every game but will rather select one of your games at random and pay you what you earn for that game.

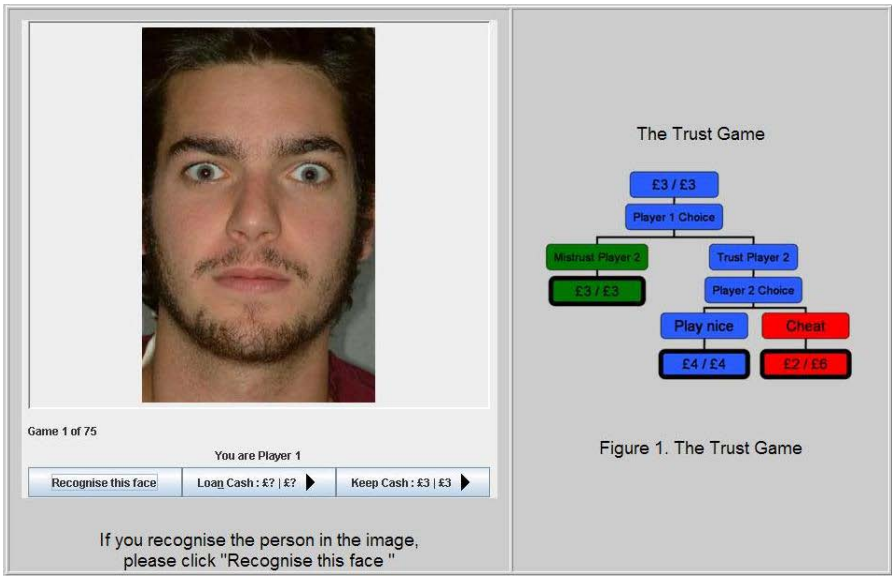
“In each game you will be allocated a counterpart. You will need to predict their possible behaviour in making a decision. You and your counterpart start this game with £3 each. The choice you face as Decision Maker 1 (DM1) is whether to give your money to them in trust.

“If you pool your resources with theirs an extra £2 will be added. Your counterpart then makes a decision (as DM2) how to distribute the pooled money. For this game they can either distribute the gains evenly (You get £4 - Figure 1: blue box) or take the majority of the cash i.e. £6 (You get £2 - Figure 1: red box).

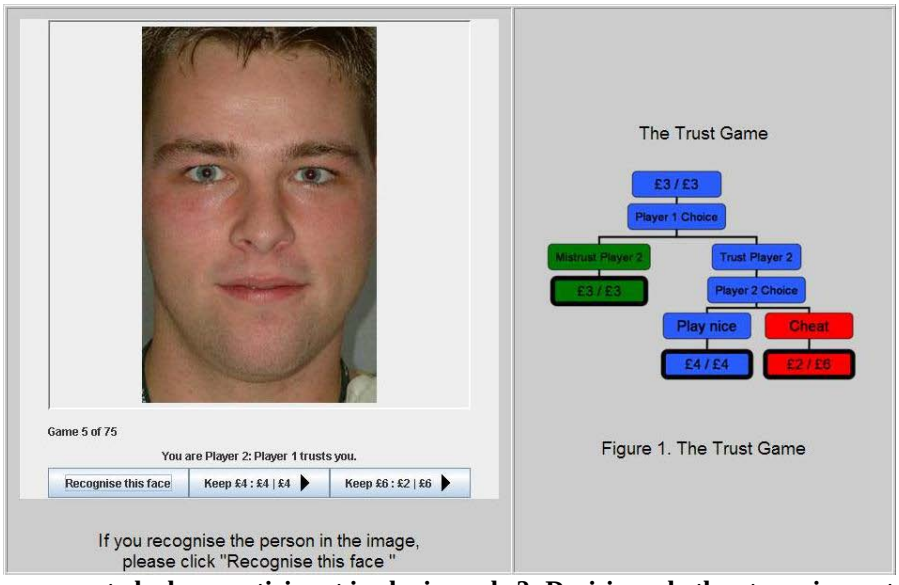
“Otherwise you can decide not to pool resources and take £3 (Figure 1: green box).

“You will play this game a number of times.”

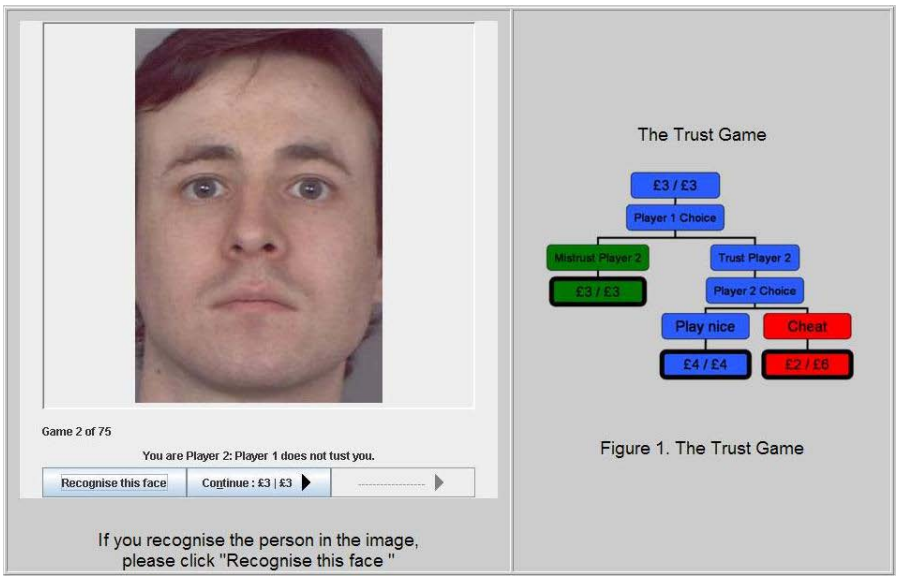
Appendix 2



Interface presented when participant is playing role 1: Decision whether to trust. Participant makes a decision whether to trust this face or not (or report that they recognise the face).



Interface presented when participant is playing role 2: Decision whether to reciprocate trust. Participant makes a decision whether to reciprocate toward this face or not (or report that they recognise the face).



Interface presented when participant is not trusted when playing role 2: Participant reports that they recognise the face or continue to next game.