FACE EVALUATION: PERCEPTUAL AND NEUROPHYSIOLOGICAL RESPONSES TO PRO-SOCIAL ATTRIBUTIONS

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A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

2013

Face evaluation: perceptual and neurophysiological responses to pro-social attributions

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This thesis is submitted in partial fulfilment for the degree of MPhil/PhD
at the
University of St Andrews

14/09/2012

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Acknowledgements

The work presented here would not have been possible without my supervisors, Dave Perrett and Ines Jentzsch, who have tirelessly guided me through the highs and lows of science, opening countless doors for me on the way. I would not be where I am today if our paths did not cross. Thank you also to Anne Perrett for editing many manuscripts and trying her best to cure me of my fondness for the word ‘however’. Unfortunately, I still use it but less extensively.

I would also like to thank my friends and colleagues (past and present) in the Perception Lab: Vinet Coetzee, Amanda Hahn, Iris Holzleitner, Carmen Lefevee, Dan Re, Michael Stirrat and Ross Whitehead. It has been fun working with all of them and discussing science ideas over a cup of coffee or around the pub table. In particular, I would like to thank Carmen Lefevre as she made the prospect of a six day working week - a pleasant idea. A special thanks to Lesley Ferrier, because everybody knows that the Perception Lab would not function without her.

I would also like to thank David Hunter, Bernie Tiddeman and Dengke Xiao for their technical help and the development of the software used in all experiments. Without their help the work presented in this thesis will not be possible.

Finally, I would like to thank my extended family for supporting me with numerous skype calls and special parcels and in particular, my fiancé who left behind his comfortable life style in Bulgaria and come here to support me through the last two years of the PhD and kept being patient even during the write-up stage.

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 with other members frequently assisting in the running of participants and the development of software. 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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Abstract

The pro-sociality of humans is manifested by the existence of cooperation in levels not common with any other species. Previous studies suggest that snap judgements of individuals are enough to determine if someone is a potential partner for cooperation. In addition to the often studied facial characteristics affecting cooperativeness and trustworthiness attribution (kin resemblance; attractiveness and emotional expression), the experimental work reported here examined the influence of head posture; gaze direction and skin colour on the attribution of trustworthiness and cooperation. A slightly tilted head (less than 3° downward) increased the perception of cooperativeness, especially for male and hostile looking faces. The importance of head tilt increased with decreased self-assessed dominance. Furthermore, even though some evidence that the effect of head posture is independent of gaze direction was found, gaze direction was also a strong indicator of cooperative intentions. Direct gaze and gaze slightly looking down (3°) were perceived as more cooperative than deviations of gaze outside this range (3° up or 6°- 9° down). Skin colour, a putative cue to current health status, was also found to impact on trustworthiness perception with a healthy skin colour increasing trustworthiness ratings. Additionally, as cooperative and trust decisions are vital for survival and social interactions, decisions based on facial appearance are made quickly and automatically as demonstrated by a trustworthiness modulation on an early face related component with 170 ms of exposure. Collectively, these findings suggest that facial characteristics employed to infer trust and cooperativeness help the observer to assess the motives and intentions of the individuals and assist the choice of partners that will lead to increased benefits

and reduced costs in collaborative actions. Such considerations fit well with the evolutionary theory of cooperation as reciprocated social exchange.

Chapter 1

Introduction to pro-social behaviour. Theories of evolution of cooperation

Humans demonstrate more complex pro-social behaviour than other mammals. Pro-social behaviour here is used to describe acts in which an individual compromises his/her own wellbeing, encounters a cost, in order to increase the welfare of another individual (i.e. benefit another individual). Examples of pro-social behaviour can be drawn from the evolutionary history (i.e. hunter-gatherer's decision to cooperate in joint parental care, territory and group defence, political coalitions, trade etc.) or in many aspects of an individual's life: elections; online purchases or any other forms of informal help such as advice, exchange of benefits, restaurant tips. Furthermore, it has even been applied to states (e.g. the formation of the European Union in 1970 to protect European countries from future war: territory and group defence; and recently creating a major market for all members: trade). This flexible pro-sociality is intriguing and needs to be further investigated. This thesis focuses on two aspects of pro-social behaviour – trust and cooperation - and in particular what facial information is used in attributing these two pro-social characteristics. Social trust and cooperation are important factors for the proper functioning of the society. People routinely decide whether to trust and whom to trust in social situations, thereby exposing themselves to the risk of loss for the possibility of greater reward. Examples of such instances are a broad range of social interactions (e.g. interpersonal - trusting a confidant; economic - trusting an investment; and etc.). As 'cooperation' can be performed in different "currencies" (food for protection; money for goods/services and etc), these acts are also referred to as 'social exchange' (Cosmides & Tooby, 1992). These terms will be used interchangeably in the thesis.

Throughout the thesis, I will argue that facial characteristics, used to perceive individuals as cooperative and trustworthy partners, guide choices that maximise the benefits or reduce the costs of the cooperative acts. I will emphasise the importance of head tilt, a nonverbal cue to display dominance, in perceiving cooperativeness. I will further explore the impact of health cues on perceived trustworthiness and examine the rapidness of the trustworthiness perception. First, three of the major evolutionary theories about cooperation will be outlined (see figure 1.1).

Theories for the evolution of cooperation

It is important to note that, in evolutionary psychology, in order for cooperation to evolve, possessing psychology driving pro-social behavour needs to improve the fitness of the individual (passing the individual's genes to future generations). One of the most widely accepted theories of evolution of cooperation is ***kin selection*** (Hamilton, 1964a, 1964b). An individual is more willing to help a closely related individual than a distantly related individual and less so to help an unrelated individual. By providing help, the individual decreases its direct fitness (i.e. reproductive success) thus incurs a cost (c) while the receiver of the help can benefit (b). Although, the direct fitness of the helper is decreased by assisting related individuals, the helper's inclusive fitness (the chance of reproducing helper's genes in further generations) is increased. Closely related individuals share more biological similarity (the amount of shared genes is higher, so the probability of having the same gene is higher). Therefore, close kin is more likely to receive help. For example, the genetic relatedness with a sibling is ½ while the genetic relatedness with a cousin is ⅛ and so on, suggesting that the sibling is most likely to be helped as its close genetic relatedness is expected to exceed the cost benefit ratio of the altruistic act ($r > c/b$). Following from this argument, kin selection theory also predicts an increase competition against individuals who are most distinctive from oneself (Hamilton, 1964a).

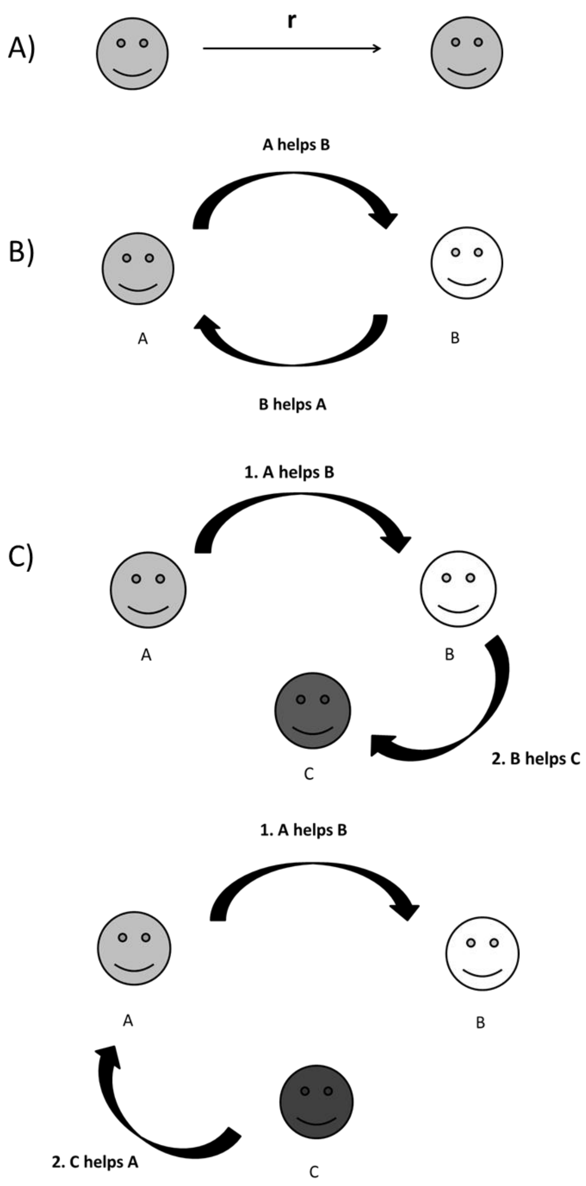

Figure 1-1. Theories for evolution of cooperation: A) **kin selection**: individuals cooperate due to genetic relatedness (r); B) **direct reciprocation**: cooperative acts are returned between the same two individuals at a later stage; C) **indirect reciprocation**: first row: cooperative acts are established as a result of a positive experience (a receiver of help might be motivated to help others); second row: cooperative acts are established as a result of reputation (a helpful individual is more likely to receive help or admiration). **Costly signalling** is related to reputation building in indirect reciprocation.

Human beings, however, do not cooperate only with related individuals. In fact, in most social groups, members other than family relatives are involved. Furthermore, cooperation can be observed not only among unrelated individuals but also among members of different species (symbiosis) (Trivers, 1971). Thus, a different mechanism is required to explain the evolution of human cooperation. One candidate theory is r***eciprocation*** (Trivers, 1971). Two forms of reciprocation are believed to promote cooperation – ***direct*** and ***indirect*** (e.g. (Nowak, 2006; Nowak & Sigmund, 1998; Trivers, 1971).

Direct reciprocation is the exchange of cooperative acts between two individuals. It assumes that individuals will interact more than once, thus performing a costly act to benefit another individual will be returned by a reciprocated cooperation at a later stage. In other words, an individual responds to actions perceived to be kind in a kind manner. Such reciprocation of pro-social behaviour is observed in species that have long life span, live in small mutually dependent groups and are characterised with low dispersal rates. There is evidence that humanoid species have met these preconditions for evolution of reciprocal cooperation (for review see Trivers, 1971). Nevertheless, it is naïve to think that human cooperation has evolved only due to the belief that a pro-social act will be returned at a later stage as there are occasions when the receiver of the cooperation is not able to reciprocate or is able to perform subtle cheating in reciprocation (i.e. attempting to provide less than what one has obtained) (Trivers, 1971).

As an alternative explanation of evolution of pro-social behaviour, an ***indirect reciprocation*** mechanism is suggested (e.g. Nowak & Sigmund, 1998). In these cases, the individual offering help is relying on building a reputation which will be rewarded by others. Providing benefits to the group increases the prestige of the individual and hence increases his/her mating opportunities. Two mechanisms can work in order to stimulate cooperation through indirect reciprocation (Nowak & Sigmund, 2005). If an individual helps another individual, the receiver, as a result of the positive interaction, can be motivated to cooperate with a third individual (Figure 1-1C first row) (Nowak & Roch, 2007). Although, this kind of reciprocity cannot allow for evolution of cooperation on its own, if it is linked to mechanism of cooperation such as direct reciprocation or network reciprocity (i.e group of individuals), it will greatly enhance the level of cooperation in a population (Nowak & Roch, 2007). Alternatively, the helper can also receive help from a different individual who was not involved in the social exchange (Figure 1-1C, second row) but observed or knew about the pro-social act.

Related to indirect reciprocation is the explanation of cooperation as ***costly signalling*** (e.g. Gintis, Smith, & Bowles, 2001; Zahavi, 1995). The cooperative act can be interpreted as an honest signal of mate quality and intentions. It is assumed that the cost of cooperation for a high quality individual is lower than the cost of cooperation for a low quality individual (Gintis, et al., 2001). Consider for example, participating in a group defence situation, which provides benefits for the group, and yet, the cost for the cooperative individual (the signaller) is smaller if the signaller possesses physical strength and dominance. By helping and cooperating, many of the helpers increase their own chances to breed. Often such costly acts are performed in front of many people rather than in front of single individual. Therefore, Zahavi (1995) argued that by investing in the welfare of another individual or the group, the helpers are advertising their quality and motives, thereby gaining ‘social prestige’.

The social prestige functions as the peacock tail [1] – it attracts collaborators and deters rivals (Gintis, et al., 2001; Zahavi, 1995). During cooperation as a costly signalling, individuals can compete with each other to invest in the interest of the group and often can interfere with others helping. Following the costly signalling theory, before entering into cooperation, humans assess the motives and qualities of the possible collaborators, advertise their own motives and qualities and then decide who to choose for a partner.

It is clear that in order to reap the benefits of cooperation, cognitive and psychological adaptations need to have evolved. Some examples of those mechanisms are the development of language that conveys the information or the "gossip" about the previous behaviour and hence reputation of the society members; increased memory that keeps track not only of the personal encounters but also of the interactions between other members of the group; a 'cheater detection' mechanism that assists computing situations when violations of the social exchange can occur (i.e. one has been cheated, Cosmides & Tooby, 1992).

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[1] The quality of the peacock tail - its size, colour, luminosity, and symmetry - serves as an honest signal of the quality of the peacock's genes to potential mates. A high-quality tail is costly to have. It takes much metabolic energy and resources to grow and maintain such an ornament, which is not useful and even can be detrimental for survival (it can be easily seen by predators). Therefore, only peacocks in good health (can acquire abundant supplies of food) and those who can survive, are able to develop such high-quality tails. As a result the tail is an honest signal of their good genes.

Other examples of psychological adaptations, which may emerge through natural selection, are the overgeneralization of attributes (i.e. babyfaced features; emotion) and a negative bias in attributing trustworthiness and cooperativeness (Van Vugt, & Van Lange, 2006). An individual whose facial features resemble a baby face configuration will be a preferred cooperative partner than an individual whose facial features are more mature. The characteristic associated with a baby – naivety; physical weakness, warmth, submissiveness – and the appropriate responses to a baby – caring; protecting; inhibiting aggression – are mirrored in impressions about baby-faced individuals (Zebrowitz & Montepare, 2006). Similarly, an individual whose facial features resemble a positive emotional expression (smile) will be also a preferred cooperative partner than an individual whose facial features resemble angry expression. The importance to ascribe the correct behavioural response (approach a smiling person and avoid an angry individual) to individuals expressing these emotions, shapes a preparedness to overgeneralise this behaviour to individuals whose features only resemble the emotional expression.

To explain the negative bias in attribution of cooperative intent, let us consider the costs that an individual encounters if wrong decisions are taken during cooperation. Trusting someone who is believed to be a co-operator but in fact is not going to reciprocate is more detrimental than not trusting someone who is believed to be a non-cooperator, but in reality is a trustworthy individual. Due to this asymmetry in cost, a strong negative bias can evolve. A typical example of a negative bias is the adaptation of females to underestimate the male’s commitment to invest in paternal care (Haselton & Buss, 2000, 2009). Another example of a negative bias is the avoidance of individuals who are physically more robust as cooperative partners, as they can potentially exploit with impunity (Stirrat & Perrett, 2010).

As outlined, it is difficult to sustain cooperation without discrimination between recipients. This is the place where the notion of trust can be introduced. Trust and trustworthiness perception can be an adaptation to protect the individual from engaging in interactions with poor exchange partners or individuals who are not willing to reciprocate (Trivers, 1971; van Vugt & van Lange, 2006). A model of trustworthiness perception (Oosterhof & Todorov, 2008) suggests that this trait attribution is an extension of the ability to read emotional expression. Thus, it is derived from the resemblance to emotional expression and is attempting to infer behavioural intentions in order to guide approach-avoidance behaviour (Todorov, 2008). Exaggerating emotionally neutral faces along the trustworthiness continuum creates expressive faces: untrustworthy looking faces are perceived as angry while trustworthy looking faces - as happy. As a result trustworthy looking individuals can be approached and chosen as potential partners while untrustworthy looking counterparts are avoided as they can potentially inflict harm on the individual. Given the importance of trustworthiness judgements for social interactions and survival, it is not surprising that individuals attribute trustworthiness automatically (e.g. Todorov, Loehr, Oosterhof, 2010 but see Santos and Young, 2005 for weak evidence of spontaneous encoding of trustworthiness using an isolation effect [2]).

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[2] isolation effect – events (stimuli) that are incongruent and rare (in numeric minority) with their prevailing context are better remembered than the surrounding items and a proper control item. The paradigm was introduced by von Restorff (1933).

Converging evidence for automatic processing of trustworthiness are provided from the neuroscience literature (e.g. Winston, Strange, O'Doherty, & Dolan, 2002). In particular, the amygdala – a structure involved in social processing (Adolphs, 2010) – is responsible for the implicit (automatic) processing of trustworthiness while superior temporal sulcus – a structure involved in processing of the changeble aspects of the face (e.g. emotional expression; gaze direction; movements (Haxby, Hoffman, & Gobbini, 2000) - is recruited during explicit judgements of trustworthiness (Mattavellli, Andrews, Asghar, Towler, & Young, 2012; Winston, Strange, Doherty, & Dolan, 2002; for a detailed discussion of the brain regions involved in and further evidence for spontaneous processing of trustworthiness perception see chapter 6). In fact, a transcranial magnetic stimulation study suggested a critical involvement of right superior temporal sulcus in explicit judgements of trustworthiness (Dzhelyova, Ellison, & Atkinson, 2011).

In many situations individuals are encountered for the first time and there is no information about reputation. On such occasions, trustworthiness perception can be based on facial appearance. Structural and emotional cues are the main sources of information for forming trustworthiness impressions (Oosterhof & Todorov, 2008). The structural cues can relate to shape difference between female and male faces or age (maturity), while the expressive cues resemble changes in the facial features conveying emotional expression (for a detailed description of facial aspects influencing trustworthiness attribution see chapter 2). Santos and Young (2011) reported that trustworthiness attributions, based on the whole face or images only of the internal facial features, are performed equally efficiently. Furthermore, the eye and the mouth region of a face contribute more to the trustworthiness perception than the upper face region (forehead). Besides face shape and configural cues impacting on trustworthiness perception, recent literature acknowledges the importance of texture and skin tone information for forming this trait attribution (Santos & Young, 2008; Todorov & Oosterhof, 2011, see also chapter 6).

Empirical investigation of trust

Most of the studies investigating trustworthiness perception have employed a rating task or a two alternative force choice (trustworthy vs untrustworthy). A different experimental approach to investigate cooperation and trustworthiness is the economic games. The economic games are often used as an operational measure of trust and cooperation. Four commonly employed games will be introduced in the following section.

Economic games

Public goods game

In the public goods game, a group of individuals (N) receives an endowment and each player can independently decide whether he/she wants to contribute any amount of the endowment to a common pool. The rest of the money is kept by the participant. The decisions are done simultaneously and anonymously. The amount of money contributed to the pool is multiplied by a factor **a** (**a** is smaller than N). In some modifications of the game, the pool has to exceed a certain amount (threshold) before it is multiplied by the factor. This restriction imposes a minimal donation amount. The resulting sum is distributed equally among all members regardless of their initial contribution. Because as a benefit to any invested amount, the individual receives a/N, a maximizing outcome strategy is not to invest in the common pool.

<u>Prisoner's Dilemma</u>

The name of the game derives from anecdotal story about two prisoners who have jointly committed a crime and have been apprehended. The District Attorney cannot prove their guilt and can only convict them if one or both confess their crime. He is questioning the prisoners individually without any opportunity for them to communicate with each other. Each prisoner is given a deal:

1) If you confess and the other prisoner does not – you will go free while the other prisoner will receive the maximal sentence.
2) If both of you confess – both of you will receive moderate sentences.
3) If none of you confesses – both of you will get the minimal sentence.

In each case, the dominant strategy is to confess as the individual will perform better: if the accomplice confesses as well the prisoner will get the moderate rather than the maximal sentence while if the accomplice does not confess the prisoner will go free rather than have a moderate sentence. However, the dilemma results from the fact that duel confession leads to a moderate sentence while no confession leads to a minimal sentence.

In economic terms, the two individuals can each choose whether they want to cooperate or to defect (not cooperate) and each is awarded a sum of money dependent on their interaction. None of them knows the choice of the other counterpart. There are several possible outcomes: (a) both players cooperate - mutual cooperation - the sum of money is divided equally by the two players; (b) only one of the players cooperates while the other one defects - unilateral cooperation (unilateral defection) - the cooperater gains nothing while the non-cooperater gains the whole sum of money; and the last possible outcome is when (c) both players do not cooperate - mutual defection – than both will gain a small sum of money, which is smaller than the one that can be gained by mutual cooperation (see Figure 1-2). Regardless of the partner's choice, the best option in Prisoner's Dilemma game is to defect since it yields higher payoff. Yet, if both partners defect, both do worse than if they both had cooperated.

		Player B	
		cooperate	do not cooperate
Player A	cooperate	**2**, **2**	**0**, **5**
	do not cooperate	**5**, **0**	**1**, **1**

Figure1-2. Example payoff matrix for the Prisoner's Dilemma. The payoff matrix for follows the rule: unilateral defection (not cooperate; cooperate) > mutual cooperation (cooperate; cooperate) > mutual defection (not cooperate; not cooperate) > unilateral cooperation (cooperate; not cooperate).

The game could be played sequentially or simultaneously and as multiple or one-shot interactions with the same partner. The optimal strategy within an iterated game was Tit for Tat (Axelrod & Hamilton, 1981). This is a simple strategy which starts with cooperation and then, the player does what the partner did in the previous move. Thus, the strategy honours cooperation and punishes defection. As a result, cooperation is established by reciprocation. The problem is that once a defection has occurred – even by mistake – the players are locked in series of defective acts (vendettas) until one of them cooperates (Nowak & Sigmund, 1993). An alternative model suggested that win – stay, lose – shift strategy, in which a player repeats the previous choice if it was successful but switches if it was not beneficial, outperforms Tit for Tat (Nowak & Sigmund, 1993). The reasons for the better performance are that the strategy 1) protects against exploitation; 2) corrects mistakes and 3) exploits a naïve co-operator (Nowak & Sigmund, 1993; Nowak, 2006; Trivers, 2005).

Trust Game

The Trust Game is a two stage game, also played by two individuals. One of the players has the role of the trustee (recipient) and the other is the investor. Initially, both players are given an endowment. In some variations of the game, only the investor receives the endowment. The investor decides if he/she wants to give some money to the trustee. If money is invested than it is increased (doubled or tripled) by the experimenter, and the trustee receives the resulting sum. At the second stage, the trustee has the option either to return a portion of the money to the investor or to keep the whole sum. Rationally, the investor should not trust the recipient and not invest initially, while the recipient should keep all of the received money. Thus, the game can be employed as an operational measure of **trust** by investigating the decisions of the investor and an operational measure of **trustworthiness** by exploring the decisions of the trustee.

Ultimatum Game

In a standard Ultimatum Game, a sum of money is given to one of two players, the proposer. The proposer has to decide how he/she would like to split the money between himself/herself and the other player. After receiving an offer from the proposer, the other participant, the responder, has the opportunity either to accept the money or to reject it. An acceptance of the offer leads to a gain for both players: the responder receives the offered money, while the proposer keeps the rest of it. Conversely, a rejection leads to a loss for both of the participants since none of them receives any money. Rationally, as players interact just once, the proposer should always offer the smallest amount of money and the respondent should always accept the offer since even a small monetary gain is better than nothing.

The classical theory of economic decision-making assumes that decisions are made rationally - trying to maximise gain and minimise lost. Therefore, choosing to defect in Prisoner's Dilemma; accepting every amount of money offered in Ultimatum Game; not returning any profit in Trust Game or not contributing to the common pool in a Public Goods Game should be the rational choice of every player. However, research on this topic demonstrates results inconsistent with the rational expectations. For example, participants cooperate almost 50 % of the occasions in Prisoner's Dilemma. Clark and Sefton (2001) reported 42% of cooperation if participants had to play as a first mover in a sequential Prisoner's Dilemma game. Similarly, in Ultimatum Game, the proposer tends to offer 50% of the amount of money in order for the offer to be accepted. Proposals of less or equal to 20 % of the amount of money seem to be considered as unfair and the other participant is often motivated to punish the proposer by rejecting the offer (for an overview see Sanfey, 2007). In the early rounds of public goods games also most of the partners donate to the common pool with contributions ranging from 40% to 60 % of the endowment (Fehr & Schmidt, 1999). A meta-analysis of approximately 162 studies investigating economic behaviour in the Trust Game suggested that on average the investors trust around 50% of the initial endowment while the trustees return approximately 37% of the resulting money (Jonson & Mislin, 2011). These results suggest that factors other than pure monetary gain play a role in social interactions.

Decisions to cooperate are biased by affection, empathy and mood (Wischniewski, Windmann, Juckel, & Brüne, 2009). Furthermore, in instances where reputation can be built, cooperation is increased (Bateson, Nettle, & Roberts, 2006; Haley & Fessler, 2005). Thus for example, communicating with (Kurzban, 2001) or seeing (Witchman, 1970) a partner influences positively cooperation rates. People contribute (Bateson, et al., 2006) and cooperate (e.g. Haley & Fessler, 2005; Rigdon, Ishii, Watabe, & Kitayama, 2009) more if they were exposed to eyes looking at them. These situations can be perceived as being seen by other and thus, as opportunities to build or lose reputation (Bateson, et al., 2006; Haley & Fessler see also Fehr & Schneider, 2010), providing experimental evidence for reputation-based mechanisms for evolution of cooperation, one of the varieties of indirect reciprocation (Nowak, 2006; Nowak & Sigmund, 1998).

Additional studies have investigated how partner's personal traits and explicit social information about one's partner can influence the economic decision-making. For example, van't Wout and Sanfey (2008) suggested that the perceived trustworthiness of a partner is a strong social cue that influences decision-making. Information about partners' moral status, acquired through the previous decisions in the game (Singer, Kiebel, Winston, Dolan, & Frith, 2004) or provided explicitly by information given prior to the game (Delgado, Frank, & Phelps, 2005) effects social interactions within the course of the game. Reputation, measured as the investor's reciprocity, in a sequential Trust Game in which the same pairs of partners were playing for several rounds, predicts the change of trust by the trustee (King-Casas et al., 2005). Even facial characteristics have been suggested to influence pro-social attributions and social exchange (Hancock & DeBruine, 2003). Chapter 2 will outline some of them.

Chapters 2-6

These chapters have been embargoed at the request of the author.

Chapter 7

Temporal dynamics of trustworthiness

This chapter is based largely on work that was published in peer-reviewed journal:

Dzhelyova, M., Perrett, D. I., & Jentzsch, I. (2012). Temporal dynamics of trustworthiness perception. *Brain Research, 1435*(0), 81-90. doi: 10.1016/j.brainres.2011.11.043

The version presented here is not the final print version.

Abstract

Behavioural and neuroimaging studies suggest that the attribution of trustworthiness to faces relies on emotional and structural cues. Previous research suggests that attributions happen spontaneously and very rapidly but the precise temporal dynamics of the underlying processes are not known. We investigated the temporal dynamics of trustworthiness perception by employing scalp recorded event related potentials and evaluating effects on components previously implicated in face processing: P1 (positive component ~100 ms post-stimulus), N170 (negative deflection sensitive to faces) and a posterior-occipital negativity ~ 230 to 280 ms (early posterior negativity – EPN). Participants judged the gender and trustworthiness of female and male images manipulated to look either more or less trustworthy. The results indicated that facilitated behavioural processing (increased accuracy and shorter reaction time) of socially important stimuli – in particular males that looked untrustworthy (and should be avoided) but also females that looked trustworthy (and who might therefore be useful in cooperative ventures) – was reflected in an increased negativity of N170 amplitude over the right hemisphere. Additionally, trustworthiness continued to modulate the amplitude of the negative deflection ~ 230 to 280 ms post-stimulus during explicit judgements of trustworthiness but not during gender judgements. The results suggest that negativity accompanies the relevance of the faces (female trustworthy and male untrustworthy) that are important to remember for future social interactions.

Keywords: P1, N170, posterior-occipital negativity, trustworthiness perception

Introduction

Trait attribution models describe personality characteristics by using two dimensions – warmth/emotional valence and competence/dominance (e.g. Fiske, Cuddy, & Glick, 2007; Oosterhof &Todorov, 2008; Wiggins, 1979). The observer is thought to make rapid and automatic assessment of an individual’s intentions from the warmth dimension; and make more considered judgments of whether or not the individual is in a position to act upon his/her intentions from the competence dimension. In a recent trait attribution model, the best approximation of the warmth dimension was found to be trustworthiness perception (Oosterhof &Todorov, 2008). Trustworthiness estimation relies primarily on emotionally expressive cues (Todorov, Baron, & Oosterhof, 2008; Krumbhuber, et al., 2007; Zebrowitz, Kikuchi, & Fellous, 2010) but also utilises cues from facial structure (Todorov, et al., 2008; Stirrat & Perrett, 2010).

Exaggerating facial features along the trustworthiness dimensions in computer-generated neutral faces produced emotionally expressive faces (Oosterhof & Todorov, 2009). Untrustworthy faces appear angry and are characterised by V-shaped brows and ∩-shaped mouths while trustworthy faces appear happy and are characterised by the opposite pattern – Λ-shaped brows and U-shaped mouths. Trustworthiness can also be conveyed by variations in structural facial features such as brow ridge, cheek protuberance and chin shape (Todorov, et al., 2008) or facial width (Stirrat & Perrett, 2010). Faces with shallow cheeks, wider chins, lower eyebrows and wider faces are perceived as less trustworthy. Male facial width to height ratio correlates with actual trustworthiness in economic games (Stirrat & Perrett, 2010). The structural features conveying low trustworthiness – shallow cheeks, low eyebrow ridge (Enlow & Hans, 1996) and increased facial width (Weston, Friday, & Liò, 2007) appear to be sexually dimorphic. Female individuals have more pronounced cheekbones, the eyebrow ridge is higher and their faces are narrower. Additionally, increasing masculinity in faces decreases their perceived cooperativeness and trustworthiness (Buckingham, et al., 2006; Oosterhof & Todorov, 2008; Perrett, et al., 1998), thus it can be speculated that sex and trustworthiness are not entirely independent dimensions.

Even though trustworthiness judgements affect social and economic interactions, people's first impressions are consistent with judgements made at longer viewing duration (Todorov, Pakrashi, & Oosterhof, 2009; Willis & Todorov, 2006). Trustworthiness can be processed even when faces are presented briefly in situations that prevent an elaborated conscious experience (Todorov, et al., 2009). When very briefly primed with either a trustworthy or an untrustworthy face, participants' perception of a subsequently presented neutral face is biased towards the trustworthiness level of the prime. Taken together, the findings suggest that the process of trustworthiness attribution happens spontaneously and fairly automatically.

Converging evidence for the automaticity of trustworthiness judgements is available from the neuroscience literature. While performing a face memory task (Engell, Haxby, & Todorov, 2007) or age judgements (Winston, Strange, O'Doherty, & Dolan, 2002) of faces varying in trustworthiness, the amygdala activation increased as the trustworthiness of a face decreased suggesting an automatic involvement of the structure in implicit trustworthiness judgments. The amygdala is generally implicated in processing emotionally and socially relevant information (for an overview see Adolphs, 2010) and is suggested to assess rapidly a stimulus's emotional valence and to feed backwards to the cortical regions involved in early stages of visual perception within the ventral stream (Adolphs, 2002; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Vuilleumier & Pourtois, 2007). Patients with bilateral amygdala damage show abnormal judgements of trustworthiness and approachability for faces (Adolphs, Tranel, & Damasio, 1998). They demonstrate a general bias in attributing trustworthiness and approachability even for faces that control subjects judge as untrustworthy. This bias was especially pronounced when the most untrustworthy faces were evaluated. Additionally, some amygdala damaged patients confuse fearful and angry emotional expressions with happy expressions (Sato, et al., 2002). Collectively, these patient studies lend support to the association between emotional expression and trustworthiness attribution.

To sum up, behavioural and neuroimaging studies suggest that ascribing trustworthiness to faces relies on mainly expressive cues. Judgements happen automatically and recruit structures involved in the processing of emotion. Neuroimaging and behavioural measures provide limited information about the time course of the processes underlying trustworthiness attribution. Therefore, event related potentials (ERPs) might be better suited as a method to investigate the exact temporal dynamics of trustworthiness attribution.

A recent study investigated trustworthiness perception employing an ERP paradigm (Rudoy & Paller, 2009). It explored how "perceptual" information (a picture of a face) and "memory-based" information (trait attribution provided by an adjective describing personality) affect trustworthiness perception. The participants were tested in three phases – a learning phase in which images, classified as trustworthy, neutral and untrustworthy based on consensus ratings, were paired with either a positive or a negative word; a rating phase during which the participants had to judge on a 5-point scale the trustworthiness of the face; and a test phase during which the participants had to recall the words associated with the face. ERPs were recorded during the rating phase of the experiment. Trustworthy as compared to untrustworthy faces evoked greater positivity, 200 to 400 ms post-stimulus – at frontal electrode sites. This modulation may reflect higher cognitive evaluation rather than spontaneous stimulus driven perception. Importantly, the study did not address the relationship between sex and trustworthiness of the face. In order to address the question of the rapidness of trustworthiness attribution and the extent to which trustworthiness perception interacts with the sex of a face and modulates the ERPs evoked by faces, we employed an ERP experiment in which participants were presented with male and female faces manipulated to look trustworthy or untrustworthy and asked to judge either stimulus gender or trustworthiness. We focused our analysis on areas within the occipito-temporal sites implicated in face perception. We evaluated components related to visual and face processing P1and N170. P1 and its magnetic counterpart M100 is often suggested to be face-sensitive (e.g. Batty & Taylor, 2003; Herrmann, Ehlis, Ellgring, & Fallgatter, 2005; Liu, Harris, & Kanwisher, 2002) and commonly influenced by low level visual attributes in facial and non-facial stimuli. Furthermore, the P1 amplitude increases to attended stimuli (Clark & Hillyard, 1996) suggesting that it is a marker of attention allocation. The N170 consistently discriminates faces in comparisons to other visual objects (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Goffaux, Gauthier, & Rossion, 2003; Rossion et al., 2000; Rousselet, Husk, Bennett, & Sekuler, 2008). It is assumed to represent structural encoding of faces (Bentin, et al., 1996), including configural information of facial features (e.g. Goffaux, et al., 2003, Rossion et al., 1999). Since we were interested in evaluating the rapidness of the trustworthiness discrimination, we examined the effect of trustworthiness perception on these early components. A modulation of either Pl or N170 would argue that the perception of trustworthiness is very rapid driven by spontaneous stimulus evaluation, rather than evoked by a top down process. Additionally, as mentioned earlier, facial trustworthiness is expressed by variations in changeable (expressive) cues and invariant (structural) aspects of the face and both P1 and N170 are reported to be modulated by emotional expression (e.g. Batty & Taylor, 2003; Martens, Leuthold, & Schweinberger, 2010; Pourtois, Grandjean, Sander, & Vuilleumier, 2004;Williams, Palmer, Liddell, Song, & Gordon, 2006 though see Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003) and facial structure – attractiveness (Halit, de Haan, & Johnson, 2000) and sexual dimorphism (Freeman, Ambady, & Holcomb, 2010) . However, it is important to note that category-specific modulations of these early ERP components, especially the P1, can often be accounted for by variations in low level stimulus features (stimulus contrast, luminance, colour, etc.) between the different stimulus categories (Rossion & Caharel, 2011; Rossion & Jacques, 2008). Therefore, the interpretation of face-sensitive effects on the P1 needs to be conducted with caution.

Another component modulated by emotional expression is the early posterior negativity (EPN) peaking ~ 200 ms. An increased EPN amplitude is reported for faces expressing a happy emotion (Williams, et al., 2006) and negative expressions – fear and anger – (Martens, et al., 2010; Schupp, Junghöfer, Weike, & Hamm, 2003). A similar increased negativity over the posterior visual areas differentiated emotional (happy and fearful) from neutral expressions (Sato, et al., 2001). The EPN is also modulated by the arousing nature of visual stimuli. When people are presented with images depicting mutilation, threat or an erotic content, the amplitude of EPN is increased (Schupp, et al., 2004). In summary, EPN is modulated by the importance of the stimuli, and salient stimuli cause an increase in this component's negative amplitude. Given the importance of trustworthiness to social interactions we might expect trustworthiness to modulate the EPN evoked by faces. Being able to make trustworthiness judgements quickly is adaptive both for avoiding untrustworthy individuals but also for remembering trustworthy individuals for future cooperation.

To sum up, we investigated the rapidness of trustworthiness perception and focused our analysis on the visual (face-sensitive) components, P1 and N170, and a negative deflection after 200 ms (EPN). More specifically, since sex dimorphism is linked to trustworthiness, we expected any trustworthiness modulation of ERP components to be contingent on sex of the face.

Method

Participants

Thirty-nine participants took part in the experiment. Data from 1 participant were not recorded due to technical problems and 6 more participants were excluded from the analysis since they did not meet the minimum criteria of at least 7 correct and artifact-free trials in each analysis cell. Mean accepted trials averaged across participants separately for each experimental condition equalled 30 (*SD* = 5. 4). The remaining 32 participants (16 male), age range 17 – 47 (*M* = 24.0; *SD* = 5.8) were included in the analysis. There was no difference in the age range for female (*M* =

24.2, *SD* = 6.8) and male participants (*M* = 23.81, *SD* = 5.0). All participants were right handed except for three female participant reporting left handedness and one male reporting ambidexterity. All participants provided signed and informed consent and were paid £8 for their participation. The study was approved by the University Teaching and Research Ethics Committee at the University of St Andrews (Approval code: PS6305).

Apparatus

The stimuli were presented on an Envy 17-inch (43-cm) CRT monitor controlled by a computer. Participants were seated in a dark room with an 80-cm viewing distance to the screen. The response keys were mounted 15 cm apart in the horizontal plane of the participant.

Electroencephalographic (EEG) activity was recorded using a BIOSEMI Active-Two amplifier system with 72 Ag/AgCl electrodes. Two additional electrodes (Common Mode Sense active electrode and Driven Right Leg passive electrode) were used as reference and ground electrodes, respectively. Vertical eye movements were recorded with two electrodes positioned above and below the eyes. Horizontal eye movements were recorded with electrodes placed at the corner of each eye. EEG and electrooculogram (EOG) recordings were sampled at 256 Hz. Off-line, all EEG channels were recalculated to average reference. Trials containing eye artifacts were corrected using the adaptive artifact correction method of BESA (Ille, Berg, & Scherg, 2002).

Stimuli

Following an established method of manipulating perceived traits, 180

Caucasian faces (90 male), photographed with standard neutral expression, were transformed to look trustworthy or untrustworthy using prototype-based computer graphic transformations (Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001). The prototypes for each sex were created by averaging 10 Caucasian model faces ranging in perceived trustworthiness expressed in SD (for untrustworthy prototypes 4 models with SD = - 8, 4 models with SD = - 6, and 2 models with SD = - 5 were averaged; for trustworthy prototypes the same individuals but with SD = + 8 (4 models), with SD = + 6 (4 models) and with SD = + 5 (2 models) were averaged), developed by Todorov, et al., 2008 using FaceGen software (www.facegen.com). The original faces were transformed + 50 % (trustworthy) or – 50% (untrustworthy) by applying to them linear difference in shape of the same sex prototypes. An oval shape mask was applied so that only the face was seen (see Figure 7-1). The stimuli were converted into black and white 8 bit images and resized to 100 x 150 dpi. Measurement of image luminosity revealed images to be darker for male than female faces, $F(1, 356) = 163.87$, $p < .0001$. Skin colour is sexually dimorphic with males having darker skin which can lead to such luminous differences. Important for present purpose, however, there was no luminosity difference based on either the trustworthiness manipulation or the interaction between sex of face and facial trustworthiness ($ps > .7$) see also footnote 6.

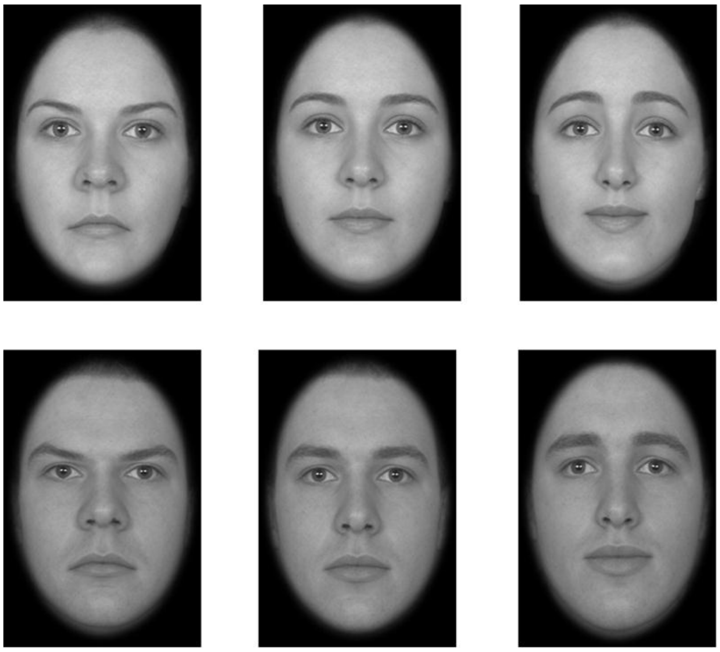

Figure 7-1. Examples of trustworthiness transformation (left: untrustworthy version (50%), mid: starting face; right: trustworthy version (50%). Note: the images are composites of 10 originally used images in the experiment

Procedure and design

Participants were instructed to respond as fast as possible while maintaining accuracy. Their task was to judge trustworthiness or gender of the images. It was stressed that trustworthiness attribution was based on their own perception. Participants responded by pressing one of two keys. In the trustworthiness discrimination task, one of the keys corresponded to trustworthy judgements while the other one corresponded to untrustworthy judgements. In the gender discrimination task, one key was assigned to female and the other key to male judgements. Key mapping was counterbalanced across participants. Half of the participants started with the trustworthiness discrimination task and the other half with the gender discrimination task. Each task was grouped in eight blocks with 45 images each. After every block, participants could take a break. The two trustworthiness versions of the same starting identity were always presented in the two different tasks and were counterbalanced across participants. Thus each participant saw all individuals twice, once in the trustworthy and once in the untrustworthy versions of the pictures. Each trial started with a fixation cross presented on the screen for 500 ms followed by an image that stayed on the screen until a response was given but no longer than 3000 ms. Responses longer than 2000 ms were rejected as too slow. The inter-trial interval was 1500 ms.

Data analysis

Behavioural data

The accuracy of responses was assessed by using a predefined classification of the images based on the direction of transformation. If the images were transformed towards an untrustworthy prototype they were predefined to be untrustworthy images. If they were transformed towards a trustworthy prototype they were predefined to be trustworthy. Only reaction times for correct responses were evaluated. Before the analysis of the data the proportion of correct responses was arcsine transformed. The reaction times were log transformed and averaged for every participant. Data transformation was performed to minimise the impact of deviation from the normal distribution. For ease of interpretation the untransformed data were presented in the figures. Preliminary analysis revealed no effect of task order or key mapping for accuracy data, nor for reaction time data. Therefore, these variables were excluded from the data analysis. A mixed ANOVA with task (gender discrimination vs. trustworthiness attribution), sex of face (female vs. male) and face trustworthiness (trustworthy vs. untrustworthy) as within subject variables and participant's gender (female vs. male) as a between subject variable was performed for the accuracy and reaction time data. Statistically significant interactions were followed up with separate ANOVAs at each level of the most theoretically relevant factor. All post-hoc analyses were Bonferroni corrected.

ERP data

The EEG recordings were examined for artifacts (amplifier blocking, scalp-muscular activity, and slow linear drift) for each participant and trial. Only trials with correct responses and without EEG artifacts were included in EEG data analysis. All signals were 0.10 – 40 Hz filtered. The stimulus-locked epoch started 200 ms prior to stimulus onset and lasted for a total duration of 1000 ms. Data were averaged separately for each condition. Visual inspection suggested that ERP waves differed between the trustworthiness levels at electrodes PO7 and PO8 in a time window 200 – 300 ms.

To analyse the effects of trustworthiness perception on early ERP components, peak amplitudes of the P1 (peak search time window 90 – 130 ms) and N170 (peak search time window 140 – 200 ms) were analysed with a mixed ANOVA. For the later component peaking at about 250 ms after stimulus onset, mean amplitudes for time windows 230 – 280 ms was used for analysis. The factors hemisphere (left vs. right) task (gender discrimination vs. trustworthiness discrimination), sex of face (female vs. male) and face trustworthiness (trustworthy vs. untrustworthy) as within subject variables and participant's gender (female vs. male) as a between subject variable were entered for all components.

Results

Behavioural data

Accuracy

The mixed ANOVA with factors task, sex of face, trustworthiness and participant's gender revealed a main effect of task, $F(1, 30) = 187.32$, $p < .0001$, $\eta_p{}^2 = .86$, $r = .93$, indicating that the gender discrimination task was performed more accurately than trustworthiness attribution. A main effect of sex of face, $F(1, 30) = 37.88$, $p < .0001$, $\eta_p^2 = .56$, $r = .75$, suggested that male faces were judged more accurately than female faces. There was a significant interaction between task and gender of the participant, $F(1, 30) = 4.71$, $p = .038$, $\eta_p{}^2 = .14$, $r = .37$, indicating that female participants responded more accurately (M = 68%) than male participants (M = 61%) in the trustworthiness judgement task, but no differences between the two sexes was observed in the gender discrimination task (females: 87 %; males: 88 %). Two two-way interactions reached significant levels: task x sex of face and sex of face x face trustworthiness, $Fs(1, 30) > 32.3$, $p < .001$, $\eta_p^2 > .52$, $r > .72$. They were further qualified by a three-way interaction, task x sex of face x face trustworthiness, $F(1, 30) = 14.51$, $p = .001$, $\eta_p{}^2 = .33$, $r = .51$. Post-hoc tests suggested the interaction between sex of face x face trustworthiness was only present in the trustworthiness discrimination task, $F(1, 30) = 37.70$, $p < .0001$, $\eta_p{}^2 = .56$, $r = .75$, but not in the gender discrimination task ($p > .05$) (see Figure 7-1). More specifically, this interaction found in the trustworthiness task was due to more accurate judgement of untrustworthy (M = 72 %) than trustworthy (M = 57%) male faces, but the opposite pattern for female faces: more accurate judgement for trustworthy (M = 70 %) than untrustworthy (M = 59 %) female faces.

Reaction times

The reaction time data mirrored the accuracy data. The ANOVA revealed a main effect of task, $F(1, 30) = 67.12$, $p < .0001$, $\eta_p{}^2 = .69$, $r = .83$, indicating that the gender discrimination task was performed faster (766 ms) than the trustworthiness attribution task (1024 ms). Additionally, responses for male faces were faster (885 ms) than female faces (905 ms), $F(1, 30) = 5.26$, $p = .029$, $\eta_p{}^2 = .15$, $r = .39$. Two two-way interactions, sex of face x task and sex of face x face trustworthiness were significant, $Fs(1, 30) > 14.98$, $ps < .001$, $\eta_p{}^2s > .33$, $rs > .58$. They were additionally qualified by the three-way interaction, task x sex of face x face trustworthiness, $F(1, 30) = 6.15$ $p = .019$, $\eta_p{}^2 = .17$, $r = .41$. Post-hoc tests revealed faster responses in the trustworthiness judgement task to untrustworthy (985 ms) than trustworthy (1072 ms) male faces, $F(1, 30) = 11.10$, $p = .008$, $r = .52$ but not female faces ($ps > .05$). No differences in trustworthiness judgement were found neither for male faces nor female faces in the gender discrimination task ($ps > .05$), see also Figure 7-2.

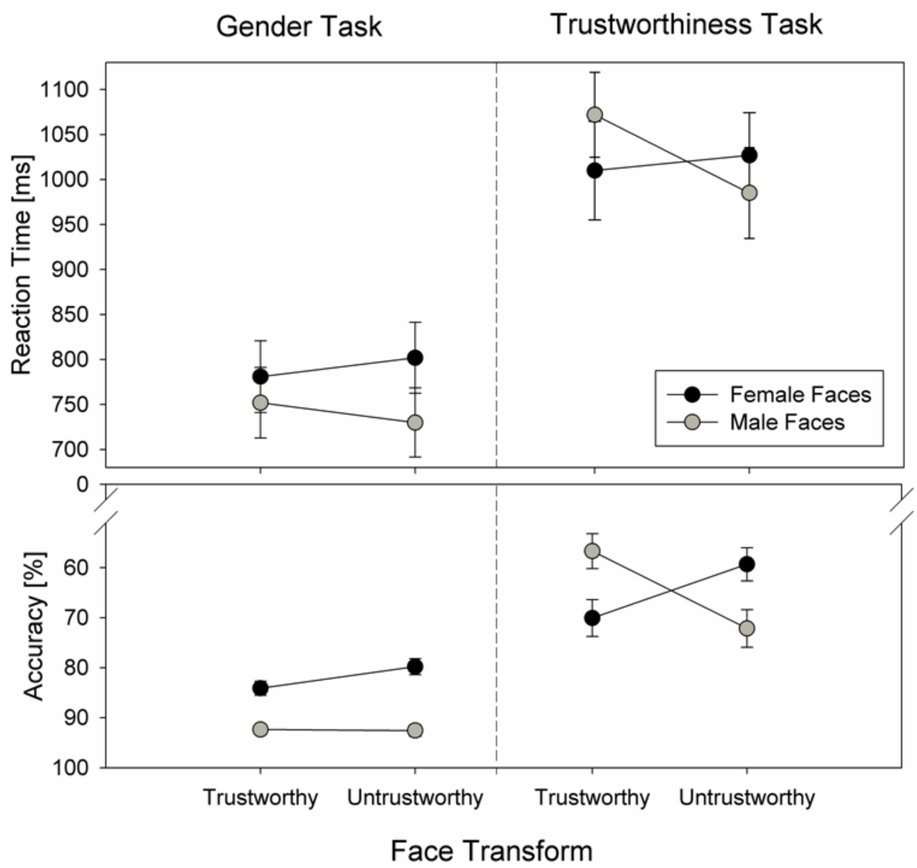

Figure 7-2. Mean reaction times (top panel) and mean proportion of correct responses (bottom panel) and corresponding SEM for the Gender Task (left panel) and the Trustworthiness Task (right panel) as a function of sex and trustworthiness of the face.

In summary, the responses in a trustworthiness judgement task were easier for trustworthy female and untrustworthy male faces as compared to untrustworthy female and trustworthy male faces, fulfilling the sex stereotyped associations (i.e. male are untrustworthy and female are trustworthy).

EEG data

Mixed ANOVAs with factors hemisphere, task, sex of face, face trustworthiness and participant's gender were conducted for all reported ERP components.

P1 amplitude

The P1 amplitude was more positive for female (10.1 μV) than male participants (5.0 μV), $F(1, 30) = 18.11$, $p < .0001$, $\eta_p^2 = .38$, $r = .61$ (see Figure 7-3). P1 amplitudes were larger over the right (9.3 μV) than left hemisphere (5.8 μV), $F(1, 30) = 11.86$, $p < .002$, $\eta_p^2 = .28$, $r = .53$. This effect was larger for female than male participants, resulting in a significant interaction between hemisphere and participant's gender, $F(1, 30) = 5.40$, $p < .027$, $\eta_p^2 = .15$, $r = .39$. Finally, there was a significant four-way interaction hemisphere x task x sex of face x participant's gender. However, post-hoc tests in each hemisphere did not reveal significant three-way interactions task x sex of face x participant's gender, $p > .10$. No other effects were significant.

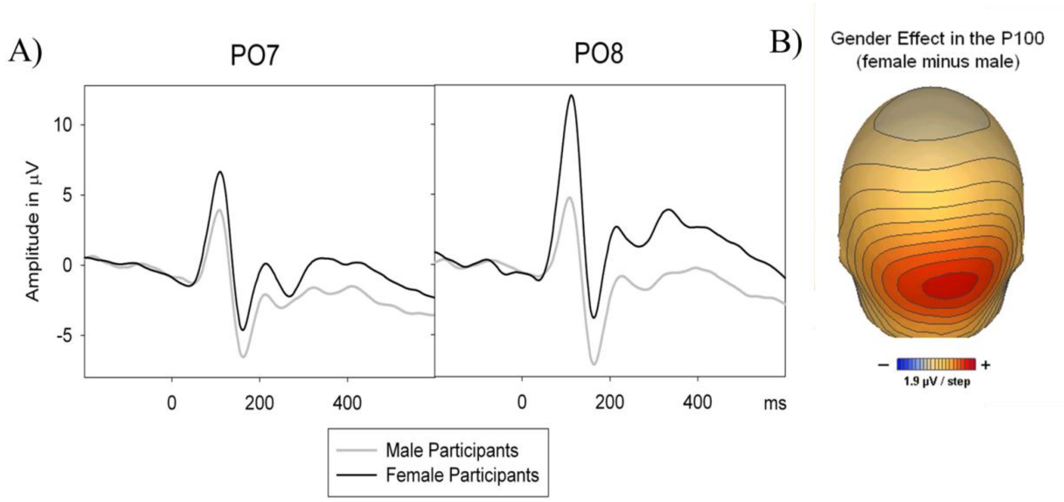

Figure 7-3. A). Participant gender differences in early visual components over posterior occipital cites PO7 (left panel) and PO8 (right panel). B) Topographic representation (Spline map) of the participant gender effect. The map depicts the difference between ERPs for female and male participants at 100 ms after stimulus onset.

N170

There was a marginally significant interaction between task and participant's gender, $F(1, 30) = 3.91$, $p = .057$, $\eta_p^2 = .12$, $r = .34$, indicating a larger effect of participant's gender in the gender discrimination task (males: $M = -8.3$, females: $M = -5.1$) than in the trustworthiness discrimination task (males: $M = -7.8$, females: $M = -5.7$). However, none of the post-hoc comparisons reached significance (*p*s > .05). Additionally, there was a trend for an interaction between hemisphere, sex of face and face trustworthiness in the N170 amplitude, $F(1, 30) = 3.33$, $p = .078$, $\eta_p^2 = .10$, $r = .32$. Separate tests for each hemisphere revealed a significant interaction between sex of face and face trustworthiness over the right hemisphere, $F(1, 30) = 7.62$, $p = .02$, $\eta_p^2 = .20$, $r = .45$, but not over the left hemisphere ($p > .10$). This interaction over the right hemisphere was due to N170 amplitudes being more negative for trustworthy female faces (- 6.9 μV) and untrustworthy male faces (- 7.1 μV) than for untrustworthy female faces (- 6.6 μV) and trustworthy male faces (- 6.6 μV) (see Figure 7-3), corresponding to the behavioural bias to perceive female faces as more trustworthy and male faces as more untrustworthy. No other effects reached significant levels (all *p*s >. 09).

EPN component (230 – 280 ms)

The ANOVA of the EPN component revealed a main effect of hemisphere, $F(1, 30) = 18.84$, $p < .0001$, $\eta_p^2 = .39$, $r = .62$, indicating that the component was more negative over the left (- 2.2 μV) than the right hemisphere (+ 0.1 μV). There was a significant three-way interaction between task, sex of face and face trustworthiness, $F(1, 30) = 4.38$, $p = .045$, $\eta_p^2 = .13$, $r = .36$. Mimicking the behavioural results, post-hoc tests revealed that the interaction between sex of face and face trustworthiness was only present in the trustworthiness discrimination task, $F(1, 30) = 8.65$, $p = .006$, $\eta_p^{\,2} = .22$, $r = .47$, but not the gender discrimination task, p > .10. The interaction in the trustworthiness task was due to ERP amplitudes being more negative for trustworthy female faces (- 1.8 μV) and untrustworthy male faces (- 1.5 μV) than for untrustworthy female faces (- 1.0 μV) and trustworthy male faces (- 0.8), (see Figure 7-4 and Figure 7-5.).

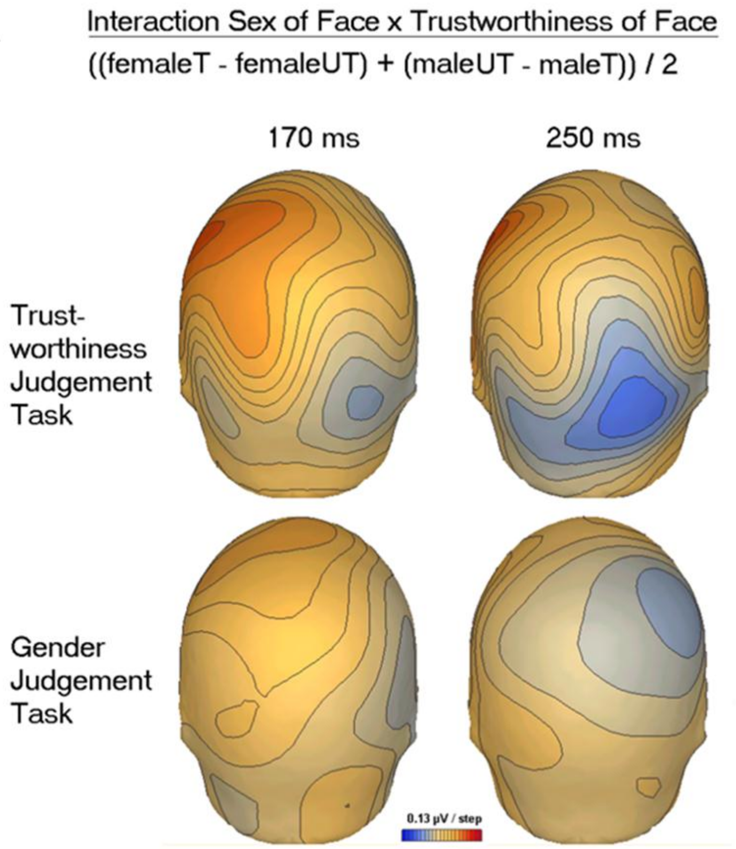

Figure 7-4. Topographic representation (spline maps) of the interaction Sex of face x Trustworthiness of face (average of (female Trustworthy minus female Untrustworthy) and (male untrustworthy minus male trustworthy), for each task separately at time points 170 ms and 250 ms after stimulus onset. T – Trustworthy; UT – Untrustworthy

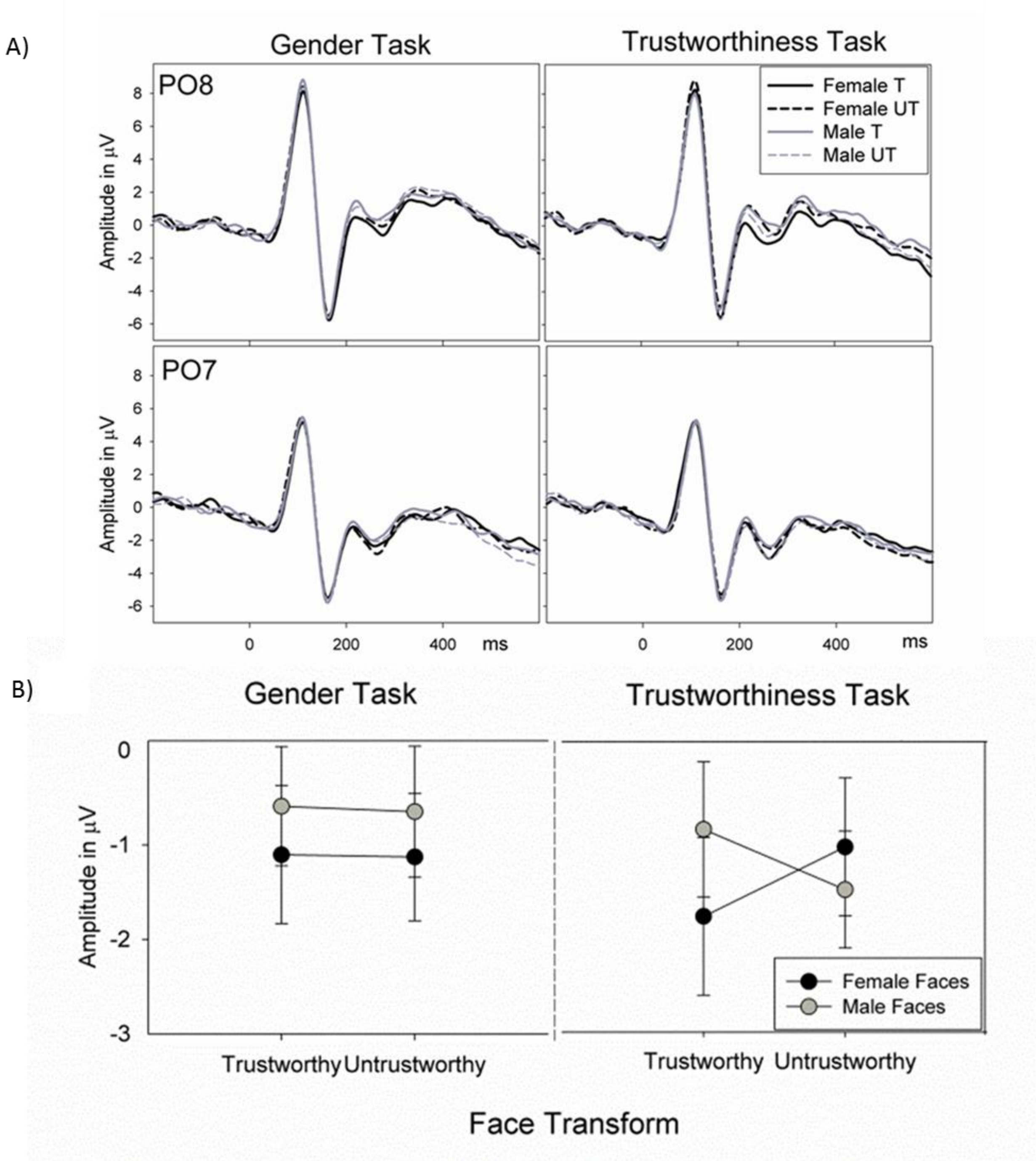

Figure 7-5. ERP modulation as a function of sex of face and trustworthiness transformation. A) Mean ERP waveforms at PO7 and PO8, shown separately for each task, with waveforms for conditions sex of face and face trustworthiness superimposed in each graph. F – Female Faces; M – Male Faces. B) Mean ERP amplitudes averaged over hemispheres, in a time window 230 to 280 ms after stimulus onset, as a function of sex and trustworthiness of the face, measured separately for each task.

To further explore the interaction between sex of face and facial trustworthiness, we tested whether the increase of the negativity in the time window 230 -250 ms correlated with the behavioural responses. The behavioural bias was calculated by averaging the accuracy levels or reaction times for the difference between faces consistent with the bias and faces inconsistent with the bias – ((female trustworthy – female untrustworthy faces) + (male untrustworthy – male trustworthy))/2. The same procedure was applied to calculate the changes in the ERP-specific bias (see also Figure 7-4). First, the increases in EPN amplitude corresponding to the behavioural bias was calculated for each hemisphere. The two ERP-specific biases for each hemisphere were averaged to produce the change of the ERP-specific bias. Each participant thus contributed to two measures of behavioural bias and one measure of ERP-specific bias (increase in EPN amplitude). The behavioural bias based on accuracy level was positively correlated with the ERP-specific bias, r = .38, p =. 031, N = 32. The correlation between the behavioural bias based on reaction time and the ERP-specific bias did not reached significance.

Discussion

Here we studied the temporal dynamics of trustworthiness perception and how sex and trustworthiness of a face modulate ERPs evoked by faces. We manipulated images to look either more trustworthy or more untrustworthy and asked participants to judge their gender and trustworthiness. We expected that the spontaneous trustworthiness perception would be reflected in the ERP components, P1and N170, and posterior-occipital negativity (EPN) after 200 ms post-stimulus. We also hypothesised that due to the relationship between trustworthiness and sexually dimorphic features the trustworthiness modulation might be contingent on the sex of the face.

From our behavioural measurements it emerged that the trustworthiness transformation affects male and female faces differently. There was a general bias to regard male faces as untrustworthy and female faces as trustworthy. Facial transformations congruent with this bias improve accuracy and speed of decisions. The bias to regard male faces as untrustworthy and female faces as trustworthy can also be described reciprocally as a tendency to see untrustworthy faces as male, whereas trustworthy faces are seen as female. Congruent transformations of trustworthiness improved gender discrimination; enhancing untrustworthiness makes the faces look more male and conversely enhancing trustworthiness makes the faces more female. This evidence further supports the relationship between sex and trustworthiness. Sex-typical features bias the perception of trustworthiness, for instance increasing the masculinity of faces decreases the perception of trustworthiness (Buckingham, et al., 2006; Oosterhof & Todorov, 2008; Perrett, et al., 1998). Furthermore, as argued in the introduction, the structural features conveying trustworthiness are suggested to be sexually dimorphic (Enlow & Hans, 1996; Stirrat and Perrett, 2010; Weston, et al., 2007).

Our EEG data suggested that trustworthiness did not affect the P1component. However, the P1 was modulated by participant's gender, with larger P1 amplitudes for female than male participants, especially over the right hemisphere. The gender specificity of this effect excludes the possibility that low-level stimulus differences account for it, as the same stimulus material was used for male and female participants. Further studies are required to explore possible gender differences in perceptual experiments using a wider variety of face and non-face stimuli.

The behavioural bias of improved performance for untrustworthy male faces and trustworthy female faces for the trustworthiness discrimination task was reflected in the amplitude of two later ERP components, the N170 and a negative deflection from 230 to 280 ms, with more negative amplitudes for faces congruent with the bias (i.e. trustworthy female and untrustworthy male faces) than faces not congruent with the bias. The interaction between trustworthiness and sex of face found for the amplitude of N170 was only present over the right hemisphere. The results suggest a rapid and spontaneous processing of trustworthiness. Right-lateralised face processing is consistent with numerous fMRI (e.g. Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & Macdonald, 1992) and ERP studies (e.g. Rossion, et al., 1999, Rossion, Joyce, Cottrell, & Tarr, 2003; Bentin et al., 1996; Bötzel, Schulze, & Stodieck, 1995). Additionally, a stronger activation within the amygdala and the superior temporal sulcus (STS) in the right hemisphere during automatic perception of trustworthiness has been reported (Engel, et al., 2007; Winston et al., 2000). Our result also fit with recent findings of a larger N170 for sex typical than sex atypical faces (Freeman, et al., 2010). Since trustworthy transformations boost the femininity of faces and untrustworthy transformations increase the masculinity of faces, the modulation of N170 we report may reflect the same process. Taken together, our N170 findings and Freeman et al.'s (2010) results suggest that the social categorization of faces occurs at an early stage of processing or perhaps during the structural encoding of the face. The results question the Bruce and Young's face perception model (Bruce & Young, 1986) indicating that there might be a cross talk between different types of social information, namely between gender and emotion (or trustworthiness). However, as effects in early visual components can often be attributed to differences in low level stimulus features (e.g., stimulus contrast, luminance, colour, etc.) our N170 results should be considered with caution. Nevertheless, given that the effects found in the N170 amplitude were not present in the earlier P1 analysis, we see this explanation as unlikely.

Importantly, the amplitude of a later (230 – 280 ms) negative deflection (EPN) was also contingent on both the sex and trustworthiness of the face. The EPN was more negative for trustworthy than untrustworthy female faces yet showed the opposite pattern for male faces with greater negativity to untrustworthy than to trustworthy male faces. This effect was only present for trustworthiness but not gender judgements. This task-specificity of the effect is important as it rules out differences in stimulus material producing this effect, as the same stimulus material was used for both tasks. Recently, an investigation exploring political elections reported an increased desynchronisation within the lower alpha band over neighbouring parieto-occipital areas for candidates judged to be trustworthy (Vecchiato, et al., 2010), thus arguing that posterior occipital regions are implicated in trustworthiness perception.

Trustworthiness attribution has an important role in the assessment of others – if they are friends or foes, approachable or unapproachable. We have reasoned that being able to make such judgements quickly is adaptive both for avoiding untrustworthy individuals but also for remembering trustworthy individuals for future cooperation. We interpret the negativity recorded at latencies 230 – 280 ms during explicit trustworthiness judgements to reflect an increased depth of processing of important faces as a result of amygdala back projections to the cortex. The amygdala feedback would reinforce the structural coding of these faces for more effective future recollection.

Salient stimuli such as emotional faces have been noted to increase the amplitude of a negative component at latencies of 200 ms (Martens, et al., 2010; Sato, et al., 2001; Schupp, et al., 2003; Williams, et al., 2006). Additionally, arousing stimuli for example, mutilation and erotic scenes modulate the amplitude of EPN (Schupp, et al., 2004). The increase in negativity for salient stimuli is often interpreted as a result of enhanced perceptual awareness of the visual stimuli (Sato, et al., 2001) and attributed to re-entrant projections from the amygdala to the cortex (Sato, et al., 2001; Schupp, et al., 2003).

Male untrustworthy faces were the most efficiently processed category. Since such males can be deemed to be the most dangerous category (looking more angry and being more capable of exploiting trust), one might expect that amygdala back projections, as part of the vigilance system, to have the largest effect on this category. On the other hand, overall, female faces were perceived as more trustworthy than male faces. We speculate that trustworthy female faces are important to process deeply in order to enhance memory for their identity. These are individuals with whom the observer is most likely to have beneficial future interactions. Our findings are consistent with other studies reporting an increase in negativity 250 ms post-stimulus accompanying deeper processing of important stimuli (e.g. Bentin & Deouell, 2000; Tanaka, Curran, Porterfield, & Collins, 2006; Schweinberger, Huddy, & Burton, 2004). Such processing potentially reflects a recognition bias induced by the participants' associations based on stereotypes. Collectively, it can be speculated that male untrustworthy and female trustworthy faces are processed deeper. This deeper processing was also reflected in the positive relationship between the increased negativity of the EPN (230-280 ms) and the increased accuracy for those stimuli.

Conclusion

The reported study found that P1amplitude was larger for female participants, particularly over the right hemisphere. Facial features related to trustworthiness affected the amplitude of N170 over the right hemisphere, thus suggesting a rapid processing of trustworthiness. The discrimination of trustworthiness characteristics continued to affect scalp-recorded negativity 230 – 280 ms. For both components – N170 and EPN – an amplitude increase (more negative components) was observed for both female trustworthy and male untrustworthy faces. We speculate that the negativity in the ERP, 230 – 280 ms post-stimulus during explicit judgements of trustworthiness, is driven by limbo-cortical processes monitoring stimulus salience. Furthermore, the different modulation of the face-evoked ERP components based on sex of the face reinforces the importance of gender when investigating trustworthiness perception.

[6] Data was analysed with a subset of trustworthy (110) and untrustworthy (110) images that did not differ in luminance across experimental conditions (all *p*s > .05). Analysis of the data from this subset of stimuli replicated all important aspects of our ERP findings and is reported below. P1: All results were replicated. N170: Again, all results were replicated. Moreover, the previously reported trend for an interaction between hemisphere, sex of face and face trustworthiness in the N170 amplitude now reached significant level, $F(1, 30) = 4.39$, $p = .045$, $\eta_p^2 = .13$, $r = .36$.

The ANOVA of the EPN component again overall confirmed of the results reported in the main section. There was a two-way interaction sex of face x face trustworthiness, $F(1, 30) = 5.51$, $p = .026$, $\eta_p^2 = .16$, $r = .39$, indicating more negative ERP amplitudes for trustworthy female faces (- 1.5 μV) and untrustworthy male faces (- 1.1 μV) than for untrustworthy female faces (- 1.1 μV) and trustworthy male faces (- 0.6). This interaction tended to be task-specific, $F(1, 30) = 4.38$, $p = .18$, $\eta_p^2 = .06$, $r = .36$, only being present in the trustworthiness judgement task, $F(1, 30) = 6.65$, $p = .014$, $\eta_p^2 = .18$, $r = .43$, but not the gender discrimination task, $F(1, 30) = 0.10$, $p = .75$, $\eta_p^2 = .003$.

Chapter 8

General Discussion

In this thesis, I examined how several facial cues: head posture, gaze direction and skin colour, effect trustworthiness and cooperativeness perception. These facial characteristics can guide choices that maximise the benefits or reduce the costs of cooperative acts. The cues advertise the qualities of the counterpart, and thus, the observer can choose partners with positive intentions (indicated by a positive emotion/subordination or direct gaze) and good health (yellowish skin colour) and avoid partners who can inflict cost on the individual (dominant individuals who can exploit with impunity; individuals disinterested in cooperation, or unhealthy individuals). These considerations are especially important when taking into account the mechanisms for evolution of cooperation and in particular, the mechanism of direct reciprocation (Trivers, 1971): cooperative acts are returned by the same two individuals.

In this concluding chapter, the findings of the experimental chapters will be discussed mainly within the framework of Trivers' (1971) theory for evolution of cooperation as a reciprocated social exchange. Face resemblance cues were not manipulated in the experimental chapters and as a result kin selection theory (Hamilton, 1964a, 1964b) will not be discussed in relation to the findings. Furthermore, the experimental chapters evaluated desired counterpart's characteristics from the perceiver's perspective, reputation building as a mechanism for indirect reciprocation and costly signalling theory of cooperation (Gintis et al., 2001) will also not be discussed. Additionally, some remarks on the psychological adaptations – 'overgeneralization' of attributes and 'negative bias' – will be provided. First, a brief summary of the results will be presented and then each of the cues – head posture; gaze direction and skin colour will be separately discussed.

Summary of experimental results

In the first experimental chapters investigating the effect of head posture on cooperativeness perception, I have demonstrated that a subtle downward tilt of the head is perceived as more cooperative. When participants are given the opportunity to freely adjust head tilt to make the head models look most cooperative, they tilt the head models slightly down (less than 3°). This head tilt can be interpreted as a display of willingness not to dominate the social interaction. By blurring out the eye region, some evidence that the postural effects on cooperation is primarily due to head position rather than gaze direction was provided. Additionally, characteristics of the perceiver and the counterpart had impact on the importance of the head tilt. In chapter 4, I showed that the downward head tilt was increased if the faces were perceived as unfriendly or hostile, particularly by participants who judged themselves to be subordinate. In chapter 5, when investigating the effects of gaze direction, the results revealed that gaze looking eye to eye or gaze looking slightly down were perceived as cooperative, suggesting that direct gaze is perceived to communicate approach behaviour and positive behavioural intentions. The use of the 3D images in these experimental chapters enabled me to address head tilt as a cue to cooperativeness from a new perspective and to overcome some of the disadvantages of 2D photography. Yet, 3D stimuli also introduced some limitations that could be further explored in future studies.

Cues to health were also shown to be crucial for the choice of social partners: yellow skin colour increased ratings of trustworthiness perception (chapter 6). As judgements about who you trust and cooperate with are vital for social interactions, the last experimental chapter evaluated the temporal dynamics of trustworthiness perception. The results indicated that neurophysiological components coding face processing (within 170 ms) are modulated by the perceived facial trustworthiness, providing further evidence for the automatic processing of facial trustworthiness. Additionally, facial trustworthiness continued to modulate a negative component responding to stimulus salience (within 230 – 280 ms post stimulus).

Employing computer graphics to manipulate faces along shape and colour axes provided several advantages over alternative methods: it allowed for a direct comparison of ratings within the same facial identity, thus controlling for potential artifacts associated with differences in shape or colour. Moreover, changing the colour dimension (in chapter 5) towards known optimal settings has not been done before. Admittedly, the procedure may introduce artifacts that can influence the investigated judgements. Although, this possibility has yet to be tested, I believe it is unlikely. It is not obvious that extraneous cues like yellower facial hair or increased contrast between the lips and the upper facial part, for example, will affect the social judgements in the same direction as the current results. Furthermore, increasing the yellowness in skin colour should increase negative evaluation. Indeed, lighter images (i.e. white skin colour) are shown to be more positively evaluated (e.g. Mandler, Nakamura, & Van Zandt, 1987).

Additionally, it is notable that the effect sizes of the influence of these characteristics were moderate and in some instances large (i.e. yellow skin colour accounted for approximately 11 % of the variance in the social perception of attractiveness and trustworthiness, while head tilt explained between 16% and 23% of the variance in attributing cooperativeness). This effect sizes might not seem substantial, yet it is impressive how a single characteristic like skin colour or head posture influences choice of a mate or a cooperative partner, decisions assumed to be rational and deliberate. Furthermore, these facial characteristics can still have an impact on social perception and thus effect the interaction in which an individual is involved. It is also notable, that in the reported studies only a limited number of characteristics were manipulated and in real world situations, several factors might vary thus decreasing the importance of the investigated facial aspects. Future studies can test the validity of the cues found here (head posture; gaze direction and skin colour) in real life situations and provide information about the importance of these cues as well as evidence for the 'kernel of truth' hypothesis.

Cues to trust and cooperation and theories of cooperation

Head posture

Chapter 3 argued that the impression of looking more cooperative when the head was tilted slightly down might be a result of an association with postural cues to status. For cooperation, a display of lowering the head may confirm that an individual is not a threat. Alternatively, it is possible that tilting the head down made the facial expression appear happier, hence hostile looking faces needed to be tilted further down in order to achieve the same level of friendliness and cooperativeness display. Both of these interpretations are examples of 'overgeneralization',, a principle discussed in the introductory chapter (Zebrowitz & Montepare, 2006; van Vugt & van Lange, 2006). The head tilt does not change the emotional expression, yet, it is possible that perception of the emotion is altered by the head tilt. The rotation of the head can lead to the mouth corners being perceived as curved up – a configuration of the mouth that is associated with a smile. Thus, this subtle perceptual resemblance to happiness may impact positively on the attribution of cooperation.

The head tilt is also associated with displays of dominance (Mignault & Chiodure, 2006, Hall et al., 2006). Seeking a low dominant individual as a partner for a cooperative venture will reduce the chance of exploitation since this partner will not be as able to implement hostile intentions. This interpretation is an example of the ‘overgeneralization’ and the ‘negative bias’ adaptation (van Vugt & van Lange, 2006). First, negative behaviour – aggression (e.g. Carré & McCormick, 2008); cheating (Haselhuhn & Wong, 2012); exploitation (Stirrat & Perrett, 2010); dishonesty (Perrett et al., 1998) – is associated with masculine face shape and increased levels of testosterone, and hence increased perceived dominance. Second, these negative perceptions are generalised to any dominant looking individual. Third, any subtle cues to dominance are overestimated, in order to avoid the potential cost of choosing the wrong partner. Additionally, face variations towards the negative end of the trustworthiness spectrum are more easily detected (Todorov, 2008) and similar effects could be expected for detection of uncooperativeness. As a result, a display of subordination or willingness not to dominate the interaction increases the perceived cooperation.

Further support that the lower head is used as a cue of counterpart’s positive intentions is provided from the findings that the effect of head posture is influenced both by participants’ own dominance and the perceived hostility of the counterpart. Male faces and faces that were perceived as more threatening were rotated downwards more. These findings are consistent with the general bias that male individuals are perceived as less trustworthy and less cooperative than female faces.

As summarised in chapter 2, this bias is also evident in the facial shape affecting trustworthiness perception. Prototypical male faces are perceived as less cooperative (Perrett et al., 1998) and less trustworthy (Oosterhof & Todorov, 2008, Buckingham et al., 2006) than prototypical female faces. Furthermore, social stereotypes dictate that anger displays are more appropriate for men and smiling is a requisite for women (Hess, Adams, & Kleck, 2005). Additionally, women are perceived as more affiliative, while men - as more dominant; and these two dimensions as discussed in the introductory chapter influence trustworthiness perception. These differences in perception can account for some of the experimental findings. The characteristics were employed to define the faces as hostile were dominance and emotional expression, thus male faces might have been perceived as more unfriendly and therefore rotated further down.

Further supporting evidence that the head tilt increases the perception of cooperativeness as a result of an association with decreased willingness to exploit are provided by the results that the importance of head tilt is dependent on the self-perceived dominance of the individual. The display of willingness not to dominate the interaction is less important for dominant individuals as the cost of underestimating the partners' power characteristics is lower (i.e. an uncooperative partner is less likely to be able to free ride without punishment) than for subordinate individuals (Watkins et al., Stirrat & Perrett, 2010).

Collectively, these findings suggest that the head tilt is used as a cue communicating the intentions of the potential partner. A desired partner is an individual who demonstrates a willingness not to dominate the interaction or a positive attitude towards the perceiver. Such individuals are less likely to inflict any cost to the cooperator and are more likely to reciprocate, supporting the idea that cues to trustworthiness and cooperation are guided by assessments of the partners that help to maximise the benefits and to reduce the cost of the cooperative act.

Gaze direction

Similarly to positive emotional expression, it can be speculated that direct gaze and gaze 3° down are interpreted as a communicative sign for positive attitude and are associated with approach behaviour. The reciprocated gaze leads to a mutual gaze. Thus, it will be easier for an individual to assess the real intentions of another person if the counterpart is looking at the perceiver. Furthermore, direct gaze can be interpreted as a demonstration of social engagement and intention to commit to a mutual cooperative act. Therefore, faces with direct gaze are perceived as more cooperative than faces that do not look into the regions of the partners face conveying communicative information (eyes or mouth region). Similarly to eye to eye contact, looking 3° down is perceived as cooperative. Looking 3° down is equivalent to looking at the mouth region of a person. This gaze angle may not only be perceived as looking at the person, but it can also facilitate emotional perception and speech recognition (Caldara et al., 2005). Various cues associated with displays of emotion are effecting perception of trustworthiness and cooperation (e.g. Oosterfoh & Todorov, 2008; Kumhuber et al., 2006).

To sum up, the impact of direct gaze and gaze looking 3° down suggest that the qualities and the motives of the partner are assessed before engaging into cooperative endeavour. Having a positive attitude towards a potential partner is indicated by reciprocated gaze and implies that the individual is willing to be involved in a cooperative act. Mutual regard can hint that the chances of reciprocation are larger than if an individual demonstrates no interest (averted gaze) or limited interest (proximate but still averted gaze) in the cooperative act.

Healthy skin colour

As argued in chapter 6, healthy skin colour, might be a perceptual cue guiding social interactions and the choice of partners. In chapter 6, the manipulated skin colour was empirically derived as the optimal amount of colour resulting from fruit and vegetables consumption (Stepehen et al., 2009; Whitehead et al, 2012). Carotenoids are yellow-red organic pigments which are abundant in fruit and vegetables. Thus, it can be argued that the skin colour manipulation represents changes of colour associated with carotenoid levels deposited in the skin. Throughout, the animal kingdom, bright carotenoid colouration is sexually selected (Lozano, 1994) and indicates current health condition (Vinkler, & Albrecht, 2010), this cartenoid colour in human skin might be used as an indicator of current health status in humans (Stephen et al, 2012). Carotenoid coloration is argued to be an honest indicator of quality due to a necessary trade-off between carotenoid used as antioxidants and those displayed in ornamentation (Dowling & Simmons, 2009). If healthy skin colour is an honest signal of current health, then healthy skin colour indicates several important aspects for social interactions: 1) the individual is healthy and engaging in social interaction will not infect other individuals; 2) it is possible that this individual possesses abundant resources that can be shared; and 3) it is possible that the healthy individual will live longer, leading to more opportunities for cooperation. All three aspects suggest that cues assisting the selection of a partner allow the individuals to maximise the benefits from the cooperative interactions. The last two aspects, in particular, provide evidence that cues influencing cooperation and trust decisions are affected by considerations of direct reciprocation (Trivers, 1971). These two aspects – long life duration and availability of resources - are perquisites for the evolution of direct reciprocation (Trivers, 1971).

The first point – avoidance of infection – is worth discussing in relation to mechanism associated with the 'behavioural immune system' (Schaller & Park, 2011). As briefly outlined in the experimental chapter, the 'behavioural immune system' is a psychological mechanism protecting the individual by inhibiting or avoiding contact with pathogen (Schaller & Park, 2011). More importantly, it can influence the choice of people, an individual interacts with and thus, the selection of potential partners. Similar to the choice of a social partner, the 'behavioural immune system' is a subject to a negative bias. The cost of misperceiving an infectious person as healthy is higher than the cost of erroneously perceiving a healthy person as infectious (Schaller, 2011). As a result, heuristic cues used as an indicator of health state will be exaggerated and cues to diseases will be over-perceived. It is suggested that the 'behavioural immune system' is sensitive to a broad range of superficial cues implying non-normative physical appearance. Perceptual mechanisms employed by this system will undoubtfully impact choice of social partners: unhealthy looking partners will be distinct from the normal physical appearance and will be avoided. The perception of an unhealthy individual will also be prejudiced. Conversely, partners with healthy skin are closer to the normal or even exaggerated in the positive direction 'super normal' and thus are going to be preferred. A similar effect of exaggerated positive characteristics compared to the average (norm) can be seen for attractiveness: attractive individuals are preferred as social and mate partners. Indeed healthy colour increases attractiveness perception (Whitehead et al., 2012).

Overall, using cues to health in order to select a partner provide further evidence that the choice of social exchange counterparts is based on decision processes facilitating the increase of benefits and the reduction of costs. Such considerations conform to the theory of reciprocated social exchange (Trivers, 1971) as an evolutionary mechanism for evolution of cooperation.

Automaticity of trustworthiness perception.

The modulation of trustworthiness transformation on early visual evoked potentials (170 – 250 ms) suggests a spontaneous encoding of this trait attribution. Given the vital role of trustworthiness assessment and its guiding role in approaching and avoiding behaviour, the automatic assessment of this trait is very important. Individuals with brain injuries affecting social judgments are impaired in their social life and often very vulnerable (e.g. Adolphs, 1998; Hall et al, 2004; Quadflieg, Todorov, Laguesse, &Rossion, in press). Facial features related to trustworthiness affected the amplitude of N170 (face specific component) and continued to affect scalp-recorded negativity 230 – 280 ms post stimulus. For both components, the amplitude increase (more negative components) was observed for both female trustworthy and male untrustworthy faces. These results are concordant with the interpretation that trustworthiness features and features conveying sex of face are not independent as outlined in the introductory chapter summarizing the facial characteristics impacting on trust and cooperation. Furthermore, the trustworthiness modulation of N170 suggests a rapid processing of this trait assessment. As argued in chapter 7, modulation of this face selective component, sensitive to the structural encoding of the face, suggests rapid stimulus driven evaluation rather than a top down assessment of trustworthiness.

In the experimental chapter, it was speculated that the increase of negativity of the event related potential 230 – 280 ms post-stimulus during explicit judgements of trustworthiness, was driven by limbic-cortical processes monitoring stimulus salience. Thus, the female trustworthy faces will be remembered while male untrustworthy faces will be avoided. This interpretation further supports the idea that the attributions of trustworthiness and thus cooperation are affected by processes and choices assisting decisions to increase benefits and to avoid incurring costs during the cooperative acts

Limitations and Future directions

The limitations of the present studies provide valuable opportunities for future research. The controlled experimental designs of the conducted studies can be criticised for lacking the elaborated nature of actual social interactions. Future studies can explore the validity of facial cues employed to judge trustworthiness and cooperation in natural cooperative endeavours and if people display them in everyday situations. Investigating whether head tilt is in fact a signal that is displayed to indicate willingness to engage in cooperative acts and if mutual gaze enhances cooperation are some directions for future experiments. This work, for example, may examine if people lower their heads when asked to display cooperation. Similarly, when participants are playing economic games – Prisoner's Dilemma, do people raise their head in moments of defection and non-cooperation. Such experiments will complement studies suggesting that some facial cues used as a heuristic to judge traits impacting on trust and cooperation are valid (Stirrat & Perrett, 2010; Wilson & Eckel, 2006); or are over-perceived as an indicator of a trait but in reality are not necessary displayed (Hall et al., 2006).

Another limitation can be that the coherent perception of a person is formed from numerous sources rather than based solely on facial appearance. In order to understand the mechanism for evolution of cooperation, a more elaborate picture of an individual needs to be provided. Recent studies suggest that information from the body and the face offers a more coherent perception of a person (Aviezer, Trope, & Todorov, 2012; Willis, Palermo, & Burke, 2011). Further evidence that the perception of an individual is more complex is provided by a study reporting enhanced memory for individuals that were perceived as more trustworthy but had bad traits – i.e. trustworthy looking cheaters (Suzuki & Suga, 2010). Elaborating on how cues from different sources – face, voice, behaviour etc. – are integrated in person perception is an important future perspective. Faces in real life do not just appear instantaneously, but people have the opportunity to interact with each other and gain information from different sources.

In order to fully understand the decisions guiding the choice of cooperative partners, information about the brain processes needs to be further explored. The network involved in the formation of snap judgements – face perception areas within the fusiform gyrus; amygdala and insula (e.g. Adolphs, 2002; Winston, et al, 2002; Hall et al, 2010) is extended to include areas within the prefrontal cortex and temporal parietal junction (e.g. Baron, Gobbini, Engell, & Todorov, 2011; Cloutier, Gabrieli, O'Young, & Ambady, 2011; Ma et al., 2011) in order to accommodate for situations when information about a person is updated. In the case of trustworthiness perception, patients with damage to the dorsomedial prefrontal cortex are impaired in learning affective trait associations but patients with hippocampal damage were able to learn these relations (Todorov & Olson, 2008). In a subsequent experiment (Baron et al., 2011), normal participants had to judge the trustworthiness of a face and then in a learning session they were provided with positive, negative description or no description of the faces. During the learning phase, the dorsomedial prefrontal cortex was activated. The strength of the "first impression" modulated the integration of the subsequently provided information whereby participants who were strongly affected by the "first impression of the face" were less influenced by the subsequent information.

Interestingly, during processing of incongruent information, none of the studies report activation in Anterior Cingulate Cortex, a structure involved in conflict detection. Typical tasks recruiting the anterior cingulated cortex are the Stroop task, Flanker task and Go/Nogo task in which competing information is present (for a review, see Botvinick, Cohen, & Carter, 2004). Additionally, when violation of expectations is present, for example in a gambling task, Anterior Cingulate Cortex is activated more in trials when participants were expecting to win but in fact they lost (Polezzi et al., 2008). Future studies can address the question of building a coherent picture of a person when conflicting information is presented by employing neurophysiological methods. The higher temporal resolution of this technique can also provide further information about the dynamics of the process. An event related potential, N200, has been identified to index inconsistency detection and is reported to originate from Anterior Cingulate Cortex (Botvinick et al., 2004). N200 is a negative component, peaking at central sites around 200ms post-stimulus. It reflects a response to conflict detection and is increased in amplitude for inconsistent trails. As such, N200 is a perfect candidate to evaluate updating of inconsistent information in perception of cooperativeness.

Conclusion

In summary, the work reported here demonstrates some novel cues affecting facial appearance that impact on trust and cooperation. Cues signalling positive intentions and good health are used to guide choices of cooperative partners, thus increasing benefits and reducing the cost of the cooperative act. These cues advertise the motives and intentions of the counterpart and thus inform the choice of a partner who is more likely to reciprocate in social exchange. Understanding the mechanism that are used in order to select social partner and why they have evolved as such adaptations is important as it gives the opportunities to 1) enhance personal social success; 2) avoid unfair biases based on instant judgements and 3) to promote such pro-social behaviour.

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Appendix A. Questionnaire measuring self-assessed dominance

Please, use the 7 point scale to indicate how much do you agree with the following statements:

1) **If you were engaged in a physical fight with a same-sex peer, you will probably win!**

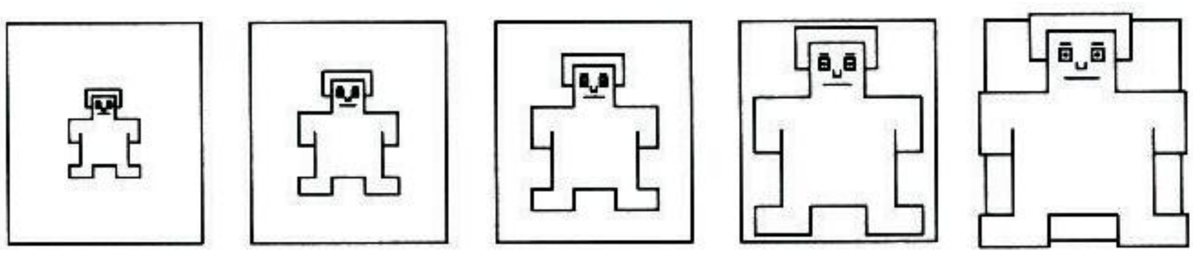
strongly disagree						strongly agree
1 ○	2 ○	3 ○	4 ○	5 ○	6 ○	7 ○

2) A **SOCIALLY DOMINANT** person tells other people what to do, is respected, influential and often a leader; while submissive people are not influential or assertive and are usually directed by others!

Based on the statement above, do you consider yourself to be:

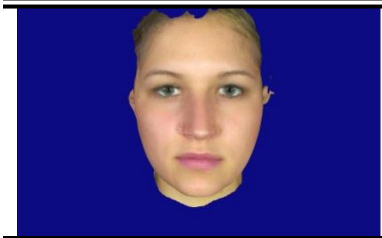
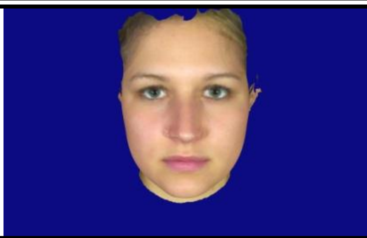
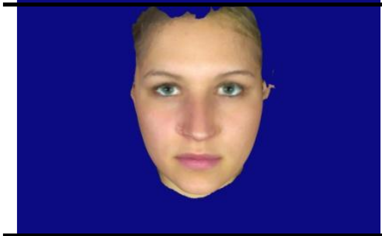
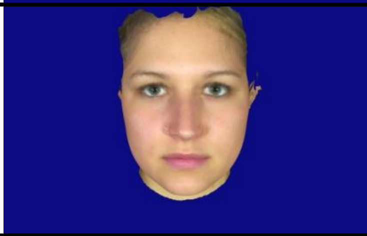
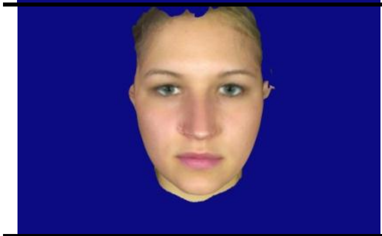
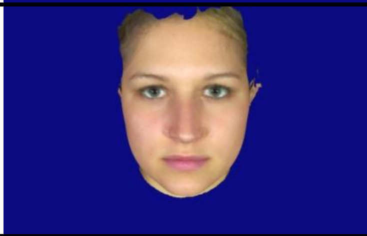
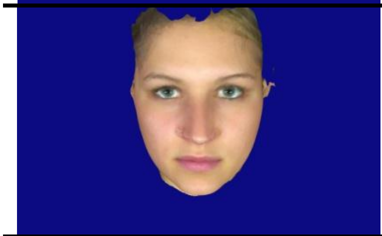
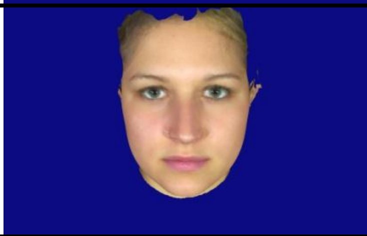
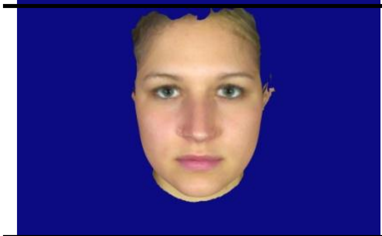
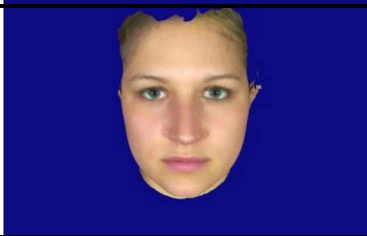
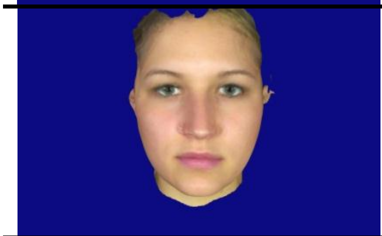
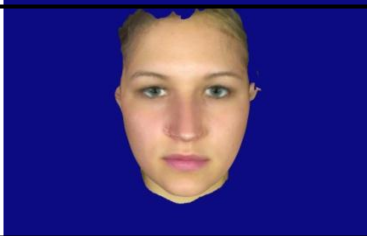
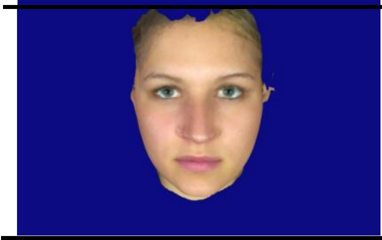
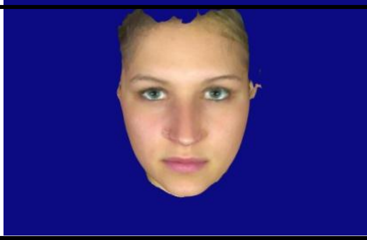
highly submissive						highly dominant
1 ○	2 ○	3 ○	4 ○	5 ○	6 ○	7 ○

3) Please indicate which figure corresponds to your self-assessed physical dominance:



○ ○ ○ ○

Appendix B. Experimental conditions in chapter 5

		**Left image**: head posture - level; gaze direction - 6° down **Right image**: head posture - level; gaze direction - 0° (looking eye to eye)
		**Left image**: head posture - level, gaze direction - up 6° **Right image**: head posture level, gaze direction - 0° (looking eye to eye)
		**Left image**: head posture -3° down ; gaze direction - down 9° **Right image**: head posture - 3° down ; gaze direction 3°down (looking to the mouth)
		**Left image:** head posture -3° down ; gaze direction - 3° up **Right image**: head posture - 3° down ; gaze direction 3°down (looking to the mouth)
		**Left image**: head posture - level; gaze direction - 0° (looking eye to eye), **Right image**: head posture 3° down; gaze direction - 3° down (looking to the mouth region)
		**Left image**: head posture level; gaze direction 6° down, **Right image**: head posture - 3° down; gaze direction - 9° down
		**Left image**: head posture - level; gaze direction - 6° up, **Right image**: head posture - 3° down; gaze direction - 3° up.

Appendix C. Ethical approvals

1. PS5970
2. PS6035
3. PS6926
4. PS7430
5. PS9129
6. PS6305

5 November 2009

Ethics Reference No: *Please quote this ref on all correspondence*	PS5970
Project Title:	Head orientation and the impression of trustworthiness
Recearchers Name(s):	Milena Dzhelyova
Supervisor(s):	Professor David Perrett

Thank you for submitting your application which was considered at the School Ethics Committee meeting on the 4th November 2009. The following documents were reviewed:

1. Ethical Application Form 04/11/2009
2. Participant Information Sheet 04/11/2009
3. Consent Form 04/11/2009
4. Debriefing Form 04/11/2009
5. Recruitment Letter 04/11/2009
6. Questionnaires 04/11/2009

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Prof. Dave Perrett (Supervisor)
School Ethics Committee

University of St Andrews

University Teaching and Research Ethics Committee

15 December 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS5970 (Amendment)
Project Title:	Head Orientation and the Perception of Trustworthiness
Researchers Name(s):	Milena Dzhelyova
Supervisor(s):	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 6th December 2010. The following documents were reviewed:

1. Ethical Amendment Form 15/12/2010
2. Participant Information Sheet 15/12/2010
3. Consent Form 15/12/2010
4. Debriefing Form 15/12/2010
5. Questionnaire 15/12/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

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Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Prof. David Perrett (Supervisor)
School Ethics Committee

University of St Andrews

University Teaching and Research Ethics Committee
School of Psychology

7 December 2009

Ethics Reference No: *Please quote this ref on all correspondence*	PS6035
Project Title:	Look at me
Researchers Name(s):	Milena Dzhelyova
Supervisor(s):	Prof. David Perrett

Thank you for submitting your application which was considered at the School Ethics Committee meeting on the 2nd December 2009. The following documents were reviewed:

1. Ethical Application Form	02/12/2009
2. Participant Information Sheet	02/12/2009
3. Consent Form	02/12/2009
4. Debriefing Form	02/12/2009

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Prof. David Perrett (Supervisor)
School Ethics Committee

University of St Andrews

University Teaching and Research Ethics Committee

27 October 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS6926
Project Title:	Facial aspects signalling cooperation
Researchers Name(s):	Milena Dzhelyova and Tim Brackfield
Supervisor(s):	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 20th October 2010. The following documents were reviewed:

1. Ethical Application Form 26/10/2010
2. Participant Information Sheets 26/10/2010
3. Consent Form 26/10/2010
4. Debriefing Form 26/10/2010
5. Invitation to Participate 26/10/2010
6. Questionnaires 26/10/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Professor David Perrett (Supervisor)
School Ethics Committee

University of St Andrews

University Teaching and Research Ethics Committee

21 April 2011

Ethics Reference No: *Please quote this ref on all correspondence*	PS7430
Project Title:	Economic Games – attractiveness and head posture
Researchers Name(s):	Milena Dzhelyova and Amanda Hahn
Supervisor(s):	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 20th April 2011. The following documents were reviewed:

1. Ethical Application Form	21/04/2011
2. Participant Information Sheet and Online Version	21/04/2011
3. Consent Form and Online Version	21/04/2011
4. Debriefing Form and Online Version	21/04/2011
5. Questionnaires	21/04/2011

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof. D. Perrett (Supervisor)
School Ethics Committee

University of St Andrews

University Teaching and Research Ethics Committee

11 September 2012

Ethics Reference No: *Please quote this ref on all correspondence*	PS9129
Project Title:	Individual differences in preference for health cues in the face
Researchers' Names:	Carmen Lefevre, Milena Dzhelyova and Amanda Hahn
Supervisor:	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 15th August 2012. The following documents were reviewed:

1. Ethical Application Form	11/09/2012
2. Participant Information Sheet	11/09/2012
3. Consent Form	11/09/2012
4. Debriefing Form	11/09/2012
5. Questionnaires	11/09/2012

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

pp Convenor of the School Ethics Committee

Ccs Prof. D, Perrett (Supervisor)
School Ethics Committee

9 April 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS6305
Project Title:	Temporal Dynamics of Trustworthiness and Gender Judgements
Researchers Name(s):	Milena Dzhelyova
Supervisor(s):	Professor David Perrett, Dr Ines Jentzsch

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 7th April 2010. The following documents were reviewed:

1. Ethical Application Form	09/04/2010
2. Participant Information Sheet	09/04/2010
3. Consent Form	09/04/2010
4. Debriefing Form	09/04/2010
5. Advertisement	09/04/2010
6. Scales	09/04/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Professor David Perrett (Supervisor)
Dr Ines Jentzsch (Supervisor)
School Ethics Committee

28 October 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS6305 (Amendment)
Project Title:	Temporal Dynamics of Trustworthiness and Gender Judgements (Ratings Task)
Researchers Name(s):	Milena Dzhelyova
Supervisor(s):	Dr Ines Jentzsch, Professor David Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 28th October 2010. The following documents were reviewed:

1. Ethical Amendment Form	28/10/2010
2. Participant Information Sheets	28/10/2010
3. Consent Form	28/10/2010
4. Debriefing Form	28/10/2010
5. Invitation to Participate	28/10/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

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Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Dr Ines Jentzsch (Supervisor)
Professor David Perrett (Supervisor)
School Ethics Committee