The effects of Attractiveness and Underlying Components on the Motivational Salience and the Memorability of Face Photographs

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Abstract

Facial attractiveness is a particularly salient social cue that influences many important social outcomes. Using a standard key-press task to measure motivational salience of faces and an old/new memory task to measure memory for face photographs, this thesis investigated both within-woman and between-women variations in response to facial attractiveness. The results indicated that within-woman variables, such as fluctuations in hormone levels, influenced the motivational salience of facial attractiveness. However, the between-women variable, romantic relationship status, did not appear to modulate women's responses to facial attractiveness. In addition to attractiveness, dominance also contributed to both the motivational salience and memorability of faces. This latter result demonstrates that, although attractiveness is an important factor for the motivational salience of faces, other factors might also cause faces to hold motivational salience.

In Chapter 2, I investigated the possible effects of women's salivary hormone levels (estradiol, progesterone, testosterone, and estradiol-to-progesterone ratio) on the motivational salience of facial attractiveness. Physically attractive faces generally hold greater motivational salience, replicating results from previous studies. Importantly, however, the effect of attractiveness on the motivational salience of faces was greater in test sessions where women had high testosterone levels. Additionally, the motivational salience of attractive female faces was greater in test sessions where women had high estradiol-to-progesterone ratios.

While results from Chapter 2 suggested that the motivational salience of faces was generally positively correlated with their physical attractiveness, Chapter 3 explored whether physical characteristics other than attractiveness contributed to the motivational salience of faces. To address this issue, I first had the faces rated on multiple traits. Principal component analysis of third-party ratings of faces for these traits revealed two orthogonal components that were highly correlated with trustworthiness and dominance ratings respectively. Both components were positively and independently related to the motivational salience of faces.

While Chapter 2 and 3 did not examine the between-woman differences in response to facial attractiveness, Chapter 4 examined whether women's responses to facial attractiveness differed as a function of their romantic partnership status. As several researchers have proposed that partnership status influences women's perception of attractiveness, in Chapter 4 I compared the effects of men's attractiveness on partnered and unpartnered women's performance on two response measures: memory for face photographs and the motivational salience of faces. Consistent with previous research, women's memory was poorer for face photographs of more attractive men and more attractive men's faces held greater motivational salience. However, in neither study were the effects of attractiveness modulated by women's partnership status or partnered women's reported commitment to or happiness with their romantic relationship.

A key result from Chapter 4 was that more attractive faces were harder to remember. Building on this result, Chapter 5 investigated the different characteristics that contributed to the memorability of face photographs. While some work emphasizes relationships with typicality, familiarity, and memorability ratings, more recent work suggests that ratings of social traits, such as attractiveness, intelligence, and responsibility, predict the memorability of face photographs independently of typicality, familiarity, and memorability ratings. However, what components underlie these traits remains unknown, as well as whether these components relate to the actual memorability of face photographs. Principal component analysis of all these face ratings produced three orthogonal components that were highly correlated with trustworthiness, dominance, and memorability ratings, respectively. Importantly, each of these components also predicted the actual memorability of face photographs.

Table of Contents

Abstract i

List of Tables v

List of Figures vi

Acknowledgments vii

Author's declaration viii

Publication statement ix

Chapter 1 General Introduction 1

1.1 Facial Attractiveness 2

1.1.1 Symmetry 4

1.1.2 Averageness 6

1.1.3 Sexual dimorphism 8

1.1.4 Skin characteristics 12

1.1.5 Eye gaze, head tilt and emotional expressions 13

1.2 Attractive faces are rewarding 15

1.2.1 Psychological components of reward 15

1.2.2 Attractive faces as a reward 19

1.2.3 Factors influencing the reward value of attractive faces 23

1.3 Facial attractiveness and memory for face photographs 26

1.3.1 Cognitive model of face recognition 27

1.3.2 Typicality, distinctiveness and memory for faces photographs 28

1.3.3 Attractiveness and memory for face photographs 29

1.4 Current research 30

Chapter 2 Women's hormone levels modulate the motivational salience of facial attractiveness 33

2.1 Introduction 33

2.2 Methods 35

2.2.1 Participants 35

2.2.2 Face stimuli 35

2.2.3 Procedures 36

2.2.4 Hormonal assays 37

2.3 Results 38

2.4 Discussion 41

Chapter 3 The motivational salience of faces is related to both their valence and dominance 44

3.1 Introduction 44

3.2 Methods **46**
3.2.1 Face-rating task 46
3.2.2 Key-press task 47
3.2.3 Initial processing of data 47
3.3 Results **49**
3.4 Discussion **54**
Chapter 4 Do partnered women discriminate men's faces less along the attractiveness dimension? **56**
4.1 Introduction **57**
4.2 Study 1 .... **58**
4.2.1 Methods 59
4.2.2 Results 60
4.3 Study 2 .... **63**
4.3.1 Methods 63
4.3.2 Results 64
4.4 Discussion **67**
Chapter 5 The components underlying traits that predict the memorability of face photographs **70**
5.1 Introduction **70**
5.2 Methods **72**
5.2.1 Participants and procedure 72
5.2.2 Data analysis 73
5.3 Results **75**
5.4 Discussion **78**
Chapter 6 General Discussion **81**
6.1 Testosterone and motivational salience **83**
6.1.1 Sex differences in the relationships between testosterone and motivational salience? 83
6.1.2 Testosterone and other types of incentives 84
6.2 Valence and memorability of face photographs **85**
6.3 Cross-cultural agreement and differences **87**
6.3.1 Symmetry 88
6.3.2 Averageness 88
6.3.3 Sexual dimorphism 89
6.3.4 Skin colouration 91
6.4 Conclusions **92**
References **93**
Supplemental Materials **123**

List of Tables

Table 3.1 Descriptive statistics for all traits considered in our analyses and results (t and p statistics) for independent samples t-tests for differences between ratings of male and female faces for each trait……………………………………………………………48

Table 3.2 Component matrix for principal component analysis of all traits….………..49

Table 3.3 Descriptive statistics of key-press scores for faces scoring ±1 SD from the mean on the valence and dominance components……………………………………...52

Table 3.4 Full results of the analysis on key-press scores …………………...................53

Table 5.1 Descriptive statistics for all traits considered in our analyses and results (t and p statistics) for independent samples t-tests for differences between ratings of male and female faces for each trait……………………………………………………………74

Table 5.2 Component matrix for principal component analysis of all traits…………..76

List of Figures

Figure 2.1 Examples of male and female faces used in the study……………………..35

Figure 2.2 Interaction between facial attractiveness and testosterone on key-press scores…………………………………………..…………………………………. 39

Figure 2.3 Interaction between facial attractiveness and testosterone on key-press scores for female faces………………………………..……………………………...40

Figure 2.4 Interaction between facial attractiveness and testosterone on key-press scores for male faces………………………………………….……………….……….41

Figure 3.1 Scatter plot of valence component versus key-press scores and the regression line between valence component and key-press scores……………………. ………51

Figure 3.2 Scatter plot of dominance component versus key-press scores and the regression line between dominance component and key-press scores……….............52

Figure 3.3 Correlation between valence component and key-press scores for female and male faces…………………………………………………………...................53

Figure 4.1 Scatter plot of men's facial attractiveness versus d-prime and the regression line between men's facial attractiveness and d-prime ……………….………………...61

Figure 4.2 Scatter plot of men's facial attractiveness versus d-prime and the regression line between men's facial attractiveness and d-prime ………………..……………......62

Figure 4.3 Scatter plot of men's facial attractiveness versus key-press scores and the regression line between men's facial attractiveness and key-press scores……………..65

Figure 4.4 Scatter plot of men's facial attractiveness versus key-press score and the regression line between men's facial attractiveness and key-press cores……….......66

Figure 5.1 Correlations between perceptual components, hit rate and false alarm rates, and d-prime……………………………………………………………..............77

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Author's declaration

I declare that this thesis is my original work carried out under the normal terms of supervision.

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Chapter 1

General Introduction

Human faces convey a great deal of information that facilitates social communication (for reviews, see Adolphs, 2001; Emery, 2000; Haxby, Hoffman, & Gobbini, 2000; Russell, 1995). People read important information from faces, such as age, sex, emotion, and familiarity. Deciphering the various signals from people's faces is a particularly important skill for successful social interaction. For instance, facial expressions of positive emotion, such as smiles, may signal trustworthiness and cooperative intent (e.g., Reed, Zeglen, & Schmidt, 2012) and encourage approach-related behaviours (Miles, 2009). However, smiles could also be faked to conceal negative emotions (e.g., Ekman & Friesen, 1982). Since interpreting the signals from others' faces correctly is central for the subsequent interaction, there has been considerable interest in understanding the psychological processes involved in face perception.

When encountering a stranger, people extract not only basic categorical information, such as sex, age, and identity, but also specific social traits, such as attractiveness and dominance (Hassin & Trope, 2000; Willis & Todorov, 2006; Oosterhof, & Todorov, 2008). Research has suggested that people make social evaluations of novel faces rapidly and automatically (Bar et al., 2006; Locher, Unger, Sociedade, & Wahl, 1993; Olson & Marshuetz, 2005; Todorov, Pakrashi, & Oosterhof, 2009; Willis & Todorov, 2006). For instance, an exposure time as little as 100-ms is sufficient for people to form impressions based on facial appearance on a variety of traits, including trustworthiness, aggressiveness, attractiveness, and competence (Willis & Todorov, 2006). Additional exposure time increases confidence in judgments but does not change the judgements significantly (Willis & Todorov, 2006).

Importantly, impressions derived from facial appearance are strong enough to have a substantial influence on people's behaviour and decision-making. For instance, perceived trustworthiness of a person's face influences the extent to which people cooperate with them in socioeconomic interactions (Van't Wout & Sanfey, 2008). The effect of perceived facial trustworthiness on cooperative behaviour is even evident in children as young as five years old (Ewing, Caulfield, Read, & Rhodes, 2015). Another example of the substantial effects of personal attributions in face perception on social outcomes is the evidence that the inferences of competence or dominance based on facial appearance can predict the election of leaders (Antonakis & Dalgas, 2009; Little, Burriss, Jones, & Roberts, 2007; Olivola & Todorov, 2010; Todorov, Mandisodza, Goren, & Hall, 2005). Moreover, young children can predict the election results based on the candidates' facial appearance in the same way that adults do (Antonakis & Dalgas, 2009).

Among the social judgements that are made from facial appearance, facial attractiveness may be the most extensively studied one. Attractiveness has important social outcomes (Dion, Berscheid, & Walster, 1972; Little, Jones, & DeBruine, 2011; Rhodes, 2006). For example, more attractive people are perceived to be more competent (Jackson, Hunter, & Hodge, 1995), more trustworthy (Mulford, Orbell, Shatto, & Stockard, 1998) and have higher salaries (Frieze, Olson, & Russell, 1989; Mobius & Rosenblat, 2006). In this chapter, I will first review the facial characteristics that contribute to facial attractiveness. Next, I will briefly introduce the literature into the reward value and memory of faces. Then I will discuss the effects of attractiveness on the reward value and memorability of faces.

1.1 Facial Attractiveness

People like attractive faces. Contrary to the common maxim that attractiveness is not important, people tend to attribute positive qualities to attractive people, which known as the "what is beautiful is good" stereotype (Dion, Berscheid, & Walster, 1972). Visual preferences for attractive faces have even been reported for 2-8 month old infants (Langlois, Ritter, Roggman, & Vaughn, 1991; Langlois et al., 1987). In addition, the correlations among attractiveness ratings are high across cultural groups (Langlois et al., 2000; Cunningham, Roberts, Barbee, Druen, & Wu, 1995), suggesting there is some degree of cross-cultural agreement on attractiveness judgements.

Facial attractiveness plays a central role in the process of impression formation (Olson & Marshuetz, 2005). For instance, attractive people are judged more positively in the domain of social appeal, academic competence, and interpersonal competence than unattractive people (see Eagly, Ashmore, Makhijani, & Longo, 1991; Langlois et al., 2000 for a review). Moreover, attractive individuals are not only perceived more favourably but also treated better than unattractive individuals (e.g., Snyder, Tanke, & Berscheid; 1977; also see Langlois et al., 2000 for a review). For example, people prefer to mate with (e.g., Kurzban & Weeden, 2005), date (e.g., Berscheid, Dion, Walster, & Walster, 1971; Stelzer, Desmond, & Price, 1987) and hire attractive individuals (e.g., Cash & Kilcullen, 1985; Marlowe, Schneider, & Nelson, 1996), rather than unattractive ones.

Why do people prefer attractive faces? Some evolutionary psychologists propose that preference for human attractiveness may reflect the psychological adaptations for mate choice (Andersson, 1994; Little, Jones, & DeBruine, 2011; Thornhill & Gangestad, 1999; Rhodes, 2006; Roberts & Little, 2008). In other words, human attractiveness judgments favour features pertaining to health and that these preferences function to enhance reproductive success (Fink & Penton-Voak, 2002; Havlicek, & Roberts, 2009; Little, Jones, & DeBruine, 2011; Roberts & Little, 2008; Thornhill & Gangestad, 1999).

Consistent with this proposal, research has shown that facial attractiveness functions as cues to health. For instance, judgments of facial attractiveness positively correlate with health perception (Jones, Little, Penton-Voak, Tiddeman, Burt & Perrett, 2001; Thornhill & Gangestad; 1999) although mixed results have been found with the associations between facial attractiveness and general health measured by medical records (Kalick, Zebrowitz, Langlois, & Johnson, 1998; Rhodes, Chan, Zebrowitz, & Simmons, 2003; Shackelford & Larsen, 1999).

Moreover, facial attractiveness predicts longevity (Henderson & Anglin, 2003), and reproductive health or fertility of women (Jokela, 2009; Law-Smith et al., 2006; Roberts, Havlicek, Flegr, Hruskova, Little, Jones, et al., 2004) and men (Jokela, 2009; Soler et al, 2003). Similarly, male facial attractiveness has also been found to be positively related to genetic diversity, especially at loci within the major histocompatibility complex (MHC), a suite of genes closely linked to immune function (Lie, Rhodes, & Simmons, 2008; Roberts, Little, Gosling, Perrett, Carter, Jones, et al., 2005). MHC-heterozygotes are linked to enhanced immunity function and therefore general health (Lie, Simmons, & Rhodes, 2009).

That people generally agree on attractiveness regardless of sex and culture gives rise to the quest for common cues that contribute to facial attractiveness. Although some theories suggest that there is no single cue that can determine attractiveness (e.g., the multiple fitness model, Cunningham, Roberts, Barbee, Druen, and Wu, 1995), there are some facial features that are generally attractive to people. The following section will discuss several cues that are commonly thought to contribute to physical attractiveness.

1.1.1 Symmetry

Humans may find symmetric faces attractive because facial symmetry advertises mate quality (e.g., Thornhill & Gangestad, 1999, Thornhill & Møller, 1997). Fluctuating asymmetries, which are random deviations from symmetry in bilaterally paired traits, are deviations from developmental stability due to the disruptive effect of both environmental (e.g., pollution, parasitism) and genetic (e.g., inbreeding, mutations) stresses during development (Møller & Thornhill, 1998; Thornhill & Møller, 1997; Van Valen, 1962). Therefore, symmetry may reflect phenotypic or genotypic quality. Humans may have evolved to favour individuals with more symmetric faces as potential mates because facial symmetry function as a signal of reproductive success. Indeed, symmetry in the real face (i.e. face images that are not manipulated, Scheib, Gangestad, & Thornhill, 1999) is preferred when it comes to the judgements of facial attractiveness (Hume & Montgomerie, 2001; Mealey, Bridgstock, & Townsend, 1999; Scheib et al., 1999).

Surprisingly, early studies investigating the relationship between attractiveness and symmetry found that people think asymmetric faces more attractive than the symmetric versions ones (Kowner, 1996; Langlois, Roggman, & Musselman, 1994; Samuels, Butterworth, Roberts, Graupner, & Hole, 1994; Swaddle & Cuthill, 1995). However, these asymmetry preferences appear to be due to the techniques the early studies used to manipulate symmetry (Rhodes, Roberts, & Simmons, 1999b). In those early studies, symmetric faces were usually created by aligning each hemiface with its mirror reflection (e.g., Kowner, 1996). As a consequence, left mirrored and right mirrored chimeric faces were created. However, these chimeric face images tended to be more abnormal and unnatural comparing to the original faces. In addition, the mirror-reflecting technique might increase the number of blemishes or spots on faces by mirroring the exact hemiface to the other side.

Studies that used a new computer graphic technique to systematically manipulate faces suggested that symmetric versions of faces were found to be consistently more attractive than the asymmetric ones (e.g., Jones et al., 2001; Little, Apicella, & Marlowe, 2007; Little, DeBruine, et al., 2011; Little & Jones, 2003, 2006; Perrett et al., 1999). Moreover, symmetry preferences have been observed in different cultures (Little, Apicella, et al., 2007). This new technique is able to remap the face image to the symmetric shape while keeping the colour and skin texture the same as the original face. The symmetric shape is calculated by averaging the position of paired features on the left and right sides of the face image. Perrett et al. (1999) found that participants preferred the symmetric faces when such a new technique was used. It is also the case when both the symmetric and original face images had the average skin texture (i.e., produced by composite or blended face images and then mapped onto the both versions of face images).

The reliable relationship between fluctuating asymmetry and developmental instability (Palmer & Strobeck, 1986) makes the evolutionary explanation of symmetry preference plausible. Consistent with this proposal, studies have suggested that people are only sensitive to the kind of asymmetry that indexes the developmental instability. Simmons, Rhodes, Peters, and Koehler (2004) showed that human faces generally had directional asymmetry (for instance, right hemiface dominance) but only the fluctuating asymmetry and random deviations from directional asymmetry contributed to perceived symmetry (Simmons et al., 2004).

Consistent with the proposal that symmetry signals mate quality, research has suggested facial symmetry may signal health. Studies have reported that symmetric faces are rated as more healthy (Rhodes et al., 2007; Rhodes et al., 2001). Moreover, Jones et al. (2001) has shown that the relationship between facial symmetry and attractiveness is mediated by perceived apparent health. However, research into the relationships between symmetry and actual health has shown mixed results. While some studies support the proposal that symmetry is related to actual health based on medical records (e.g., Thornhill & Gangestad, 2006), other studies found no correlations (e.g., Rhodes et al., 2001).

An alternative explanation for the link between facial symmetry and perceived attractiveness proposes that the preference for symmetry in the face is because symmetric patterns are easier to process. Consequently, the preference for symmetry might merely be a by-product of the general perception or recognition mechanism (e.g., Reber, Schwarz, & Winkielman, 2004). However, this point of view could not explain the sex difference of sensitivity to symmetry preference. For instance, Little, Burt, Penton-Voak, and Perrett (2001) found that heterosexual females preferred symmetry in male faces more than they preferred symmetry in same-sex faces. Collectively, these results suggest that the symmetry-attractiveness link might not simply be the by-product of the visual system.

In summary, faces that are more symmetric tend to be more attractive. Moreover, in accordance with the proposal that people prefer facial symmetry because it signals genotypic quality, humans are only sensitive to the kind of symmetry that indexes the developmental stability. However, it should be noted that symmetry is positively related to averageness (i.e., manipulations to increase facial symmetry also increase facial averageness) and the effects of symmetry may be confounded with averageness (Jones, DeBruine, & Little, 2007). Moreover, research has indicated that averageness preferences remain significant even after controlling for the contribution of symmetry. Thus, I will discuss the role of averageness in facial attractiveness in the next section.

1.1.2 Averageness

Facial averageness is also thought to be an important cue to facial attractiveness. Research into the attractiveness of facial averageness has been motivated by Francis Galton (1878), who first created the composite photograph technique to generate an average face. Galton noticed that the composite face, which was generated by overlaying several individual faces, appeared to be more attractive than the individual faces were (Galton, 1879). Consistent with the results of this pioneering study, more recent studies, using computer graphic techniques, have shown that composite faces tend to be more attractive than the component faces (e.g., Langlois & Roggman, 1990; Rhodes, Sumich, & Byatt, 1999). Consequently, Langlois and Roggman (1990) concluded that attractive faces are only average, which is referred as the averageness hypothesis (Perrett, May, & Yoshikawa, 1994).

However, there are some criticisms to the averaging technique. For instance, the composite face image that is generated by blending component faces tends to have smoother skin and more symmetric pattern of face than individual faces (Little & Hancock, 2002; Rhodes, 2006; Rhodes et al., 1999). It may also bring some non-average features to the composite face, such as large eyes. However, the attractiveness of averageness remains when controlling these confounding effects (Little & Hancock, 2002; O'Toole, Price, Vetter, Bartlett, & Blanz, 1999; Rhodes et al., 1999).

Studies using real, unmanipulated images of faces have shown converging evidence that faces that scored high on typicality (similar to averageness) tend to have higher scores on attractiveness than faces with low typicality scores (Morris & Wickham, 2001; Vokey & Read, 1992). Furthermore, recent studies that used geometric morphometric to assess facial averageness revealed a similar pattern of results (Komori, Kawamura, & Ishihara, 2009; Lee et al., 2016). Compared to the studies using manipulated face images, the effect size was smaller for the real face though (Komori et al., 2009; Rhodes, 2006). Together, these results suggest that the effect of averageness on attractiveness cannot be fully explained by the technique that was used to manipulate averageness.

An evolutionary point of view proposes that facial averageness reflects genetic heterozygosity, an index of genetic health of the potential mate, which may be beneficial for reproductive success (Lie et al., 2008; Thornhill & Gangestad, 1993). Consistent with this view, research showed that manipulated averaged faces were perceived healthier than individual faces (Rhodes et al., 2001; Rhodes et al., 2007) and facial averageness at 17 years of age was related to childhood health for males and weakly related to adolescent health for females (Rhodes et al., 2001). Recently, Lee et al. (2016) directly tested if facial averageness was heritable. While they found that facial averageness did have some heritable genetic component, there was no genetic correlation between facial averageness and attractiveness. While this evidence does not support the good genes theory, it is still possible that facial averageness is preferred because of direct benefits, such as disease resistance. Alternatively, the preference for facial averageness might just be a by-product of the visual system since the average face is closer to the prototype and thus is easier to be processed (e.g., Reber et al., 2004; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006).

Other findings, however, cast doubt on the averageness hypothesis. For instance, Perrett et al. (1994) created the '*average'* face shape by averaging the shapes of the whole sample of 60 female faces and the '*high'* face shape by averaging the 15 female faces with highest attractiveness ratings in the sample. The *'high + 50%'* face was generated by exaggerating the shape differences from the 'average' to 'high' face by 50%. All skin textures were identical for the '*average'*, '*high'*, and '*high + 50%*' face images. They found that male participants preferred the 'high' to the 'average' composite and 'high +50%' to the 'high' composite consistently and suggested that highly attractive faces were different in shape from average (Perrett et al., 1994).

Follow-up studies further tested the hypothesis that attractiveness depends on the directional distance from average (also known as the contrast hypothesis, DeBruine, Jones, Unger, Little, & Feinberg, 2007). The contrast hypothesis proposes that attractiveness does not merely depend on the deviation from the prototype but also the direction towards or away from it. The face stimulus that they used was generated by manipulating the average female composite (following Perrett,1994, the composite of 60 female faces) along the attractiveness (composite of 15 most attractive faces) dimension from -600% to +600% in 50% steps. Using both rating and forced choice paradigms, they found that attractiveness and averageness were systematically different (DeBruine et al., 2007). Using the visual adaption paradigm, different patterns of results were found for judgements of attractiveness and normality while the averageness hypothesis would predict same patterns of results for these two judgements (DeBruine et al., 2007).

In summary, faces that are closer to the average tend to be more attractive than those that deviate from the average. However, averageness alone cannot fully explain attractiveness. Research suggests that other components underlying facial attractiveness may be those that deviate systematically from averageness.

1.1.3 Sexual dimorphism

Human faces contain important categorical information, such as sex (Campanella, Chrysochoos, & Bruyer, 2001). Facial secondary sexual traits appear at puberty and their development is driven by sex hormones (Israel, 1969). Partly due to the sex hormones, male faces have relatively larger jaws, cheekbones and brow ridges compared to female faces (Thornhill & Gangestad, 1996).

1.1.3.1 Femininity and women’s facial attractiveness

Femininity is consistently preferred for female faces. Femininity is attractive in female faces from studies that either measured facial femininity (e.g., Cunningham et al., 1995; Koehler, Simmons, Rhodes, & Peters, 2004) or rated facial femininity (e.g., Koehler et al., 2004; Rhodes, et al., 2003; Rhodes et al., 2007). Similarly, studies that used the computer graphic technique to manipulate femininity / dominance found consistent results (Little, DeBruine, & Jones, 2011; Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000; Welling et al., 2008). To manipulate sexual dimorphism, male and female prototypes were first created by averaging male and female faces and then the feminised or masculinized face shape can be generated by enhancing or diminishing the face image along the sexual dimorphism dimension between the male and female prototypes (Perrett et al., 1998). Participants preferred feminised shapes of female faces to average or dominant face shapes (Perrett et al., 1998).

From an evolutionary point of view, femininity in female faces may be preferred because it signals mate quality (Fink & Penton-Voak, 2002; Little, Jones, et al., 2011; Thornhill & Gangestad, 1999). It is proposed that high levels of sexual hormones, both testosterone and estradiol, stress the immune system so that only healthy individuals can afford large sexual traits (Rhodes et al., 2003). Consistent with this claim, evidence suggests there is a link between feminine face shapes and physical health. For instance, women with relatively feminised faces are reported to have fewer respiratory infections or to recover quickly from these diseases (Thornhill & Gangestad, 2006). Similarly, Gray and Boothroyd (2012) found that women with feminised faces were reported to have less colds in the preceding twelve months and less antibiotic use in the last three years and the last twelve months. In addition, feminine female faces are perceived to be healthy for both western faces (Rhodes et al., 2007; Law Smith et al., 2006) and eastern faces (Rhodes et al., 2007). However, there are some inconsistent results. For example, Rhodes et al. (2003) found there was no correlation between rated femininity in female faces and their actual health measured by their medical examinations and health histories.

1.1.3.2 Masculinity and men’s facial attractiveness

It is less clear whether masculinity is preferred for males’ faces. Research investigating the relationship between ratings of men's facial attractiveness and their facial masculinity has shown inconsistent results. Studies using the same computer graphic technique (following Perrett et al., 1998) to manipulate femininity / dominance produced different patterns of results (i.e., using the shape difference between the female and male prototypes to manipulate face images along the sexual dimorphism dimension). Some studies found facial masculinity was preferred for men's faces by women (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Little, Cohen, Jones, & Belsky, 2007; Little, DeBruine, et al., 2011; Little, Jones, DeBruine, & Feinberg, 2008) or by both men and women (Feinberg, DeBruine, Jones, & Little, 2008). Others indicated that facial femininity was preferred for male faces by both sexes (e.g., Perrett et al., 1998) or by women (e.g., Little et al., 2001).

Trade-off theory was proposed to explain the variation in women's preferences for men's facial masculinity (Gangestad & Simpson, 2000; Gangestad & Thornhill, 2008). It is suggested that women can adopt different mate choice strategies in accordance with different circumstances. Women's mate preferences focus on two types of cues: good parenting and good genes. On one hand, research investigating the link between men's facial masculinity and good genes suggests that facial masculinity may signal immunocompetence (also known as the immunocompetence handicap hypothesis, Folstad & Karter, 1992). The disadvantage of masculinity, on the other hand, would be associated with negative attributions, such as coldness or dishonesty, that are relevant to parental investment while facial femininity might signal the qualities of good parenting (Boothroyd, Jones, Burt, & Perrett, 2007; Penton-Voak et al., 1999; Perrett et al., 1998). Women need to make trade-offs between the qualities of good genes and good parenting when it comes to mate choice.

According to the immunocompetence handicap theory, males develop the testosterone-dependent sex-typical traits to attract females at the cost of resources (Andersson, 1994). Only the high-quality male can afford high levels of testosterone required for the development of sex-typical traits. Thus, sex-typical traits such as facial masculinity can honestly signal males' genetic quality (Folstad & Karter, 1992; Muehlenbein & Bribiescas, 2005). Indeed, research has shown that facial masculinity is positively related to actual health in male adolescents (Rhodes et al., 2003) and negatively related to self-reports of respiratory disease in men (Thornhill & Gangestad, 2006). Other researchers, however, criticize the assumptions that immunocompetence handicap theory has relied on such that the effects of testosterone on immune function appear to be weak (Boothroyd, Burt, & Lawson, 2009; Scott, Clark, Boothroyd, & Penton-Voak, 2013). Recently, a meta-analysis has been conducted to test the hypothesis that testosterone suppresses immune function in males (Foo, Nakagawa, Rhodes, & Simmons, 2016). Their results suggest that while the correlational studies do not reveal significant relationships between testosterone and immune function, experimental studies show that testosterone has an immunosuppressive effect on immune function (Foo, Nakagawa, Rhodes, & Simmons, 2016), which challenges this latter position.

Consistent with the trade-off theory, evidence suggests that women are more likely to select the masculinized faces as attractive when they are in high-conception-risk phase than in low-conception-risk phase of the menstrual cycle as they can only translate a male partner's genetic health into offspring when they are fertile (Jones, Vukovic, Little, Roberts, & DeBruine, 2011; Little et al., 2002; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). Similarly, women's preferences for masculinized faces are stronger when they considering short-term relationships than long-term relationships as the potential costs of masculinity are less serious in short-term relationships (Burt, Kentridge, Good, Perrett, Tiddeman, & Boothroyd, 2007; Penton-Voak et al., 1999, 2003; Little, Jones, Penton-Voak, Burt, & Perrett, 2002). In addition, women's preferences for masculine male faces are related to their sensitivity to pathogen disgust (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010). A further piece of evidence supporting this theory is that women showed stronger preferences for masculinity in countries where health conditions were poorer (DeBruine, Jones, Crawford, Welling, & Little, 2010). While other researchers proposed that factors associated with male-male competition better explained the national variation in women's masculinity preferences (Brooks, Scott, Maklakov, Kasumovic, Clark, & Penton-Voak, 2011), further analyses controlling for these factors still confirmed a significant relationship between health and preferences for masculinity (DeBruine, Jones, Little, Crawford, & Welling, 2011).

In summary, femininity is consistently preferred for female faces. However, there are more variations in preference for masculine male faces. Trade-off theory has been proposed to explain this variability. According to this theory, women make trade-offs between facial cues to the qualities of good genes and facial cues to good parenting when it comes to mate choice.

1.1.4 Skin characteristics

While the research discussed above focuses on the influence of facial shapes (symmetry, averageness, femininity / masculinity) on facial attractiveness, skin characteristics also play a role in facial attractiveness (Jones, Little, Burt, & Perrett, 2004). As several lines of evidence have suggested a link between attractiveness and traits that are perceived as healthy, the apparent health of facial skin influences attractive judgments (Fink, Grammer, & Matts, 2006; Jones et al., 2004; Stephen, Coetzee, Smith, & Perrett, 2009). For instance, health ratings of small skin patches extracted from the left and right cheeks of male face images are positively correlated with ratings of attractiveness of the whole faces, suggesting apparent health of skin affects male facial attractiveness independently from facial shape (Jones et al., 2004). Together, these results suggest the importance of facial skin to facial attractiveness.

1.1.4.1 Skin colouration

Recent studies of facial skin coloration (Jones et al., 2015; Lefevre, Ewbank, Calder, Von Dem Hagen, & Perrett, 2013; Stephen, Coetzee, & Perrett, 2011; Stephen, Coetzee, et al., 2009; Stephen, Smith, Stirrat, & Perrett, 2009; Whitehead, Coetzee, Ozakinci, & Perrett, 2012; Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012) have measured coloration on the red (a*), yellow (b*), and light (L*) axes in CIELab colour space. Increasing facial lightness (L*) and yellowness (b*) increases the perceived health (Stephen, Law Smith, et al., 2009; Stephen, Coetzee, et al., 2011) and attractiveness (Coetzee, Scott, Coetzee, Pound, Perrett, & Penton-Voak, 2012; Whitehead, Re, et al., 2012). Increasing facial redness (a*) increases perceived health (Re et al., 2011; Stephen, Coetzee et al., 2009; Stephen, Law Smith, et al., 2009) and attractiveness (Re et al., 2011; Stephen, Oldham, Perrett, & Barton, 2012). Facial redness is proposed to be associated with oxygenated blood, thus signalling cardiovascular fitness (Stephen, Coetzee, et al., 2009), or to be related to women's current estradiol levels and may contain information about fertility (Jones et al., 2015). Facial yellowness is thought to be related to carotenoid coloration and reflect fruit and vegetable consumption (Stephen et al., 2011; Whitehead, Re, et al., 2012).

1.1.4.2 Homogeneity

Measures of skin texture’s homogeneity are also correlated with attractiveness ratings of female faces made by male participants (Fink, Grammer, & Thornhill, 2001). That is a female face with a more homogeneous (i.e. smooth) skin surface is considered more attractive than a female face rich in contrast. In addition, the homogeneity of skin colour distribution of female faces influences the perception of attractiveness, age and health (Fink et al., 2006; Matts, Fink, Grammer, & Burquest, 2007). The facial colour distribution of younger women is judged as younger, healthier and more attractive than that of older women. Recent evidence also suggested a similar effect of homogeneity of male face skin on perceived attractiveness, age and healthiness (Fink et al., 2012).

1.1.4.3 Facial contrast

The contrast between the luminance of the darker regions and lighter regions influences judgements of facial attractiveness (Russell, 2003) and health (Russell, Porcheron, Sweda, Mauger, & Morizot, 2015). Russell (2003) revealed that increasing the differences between the eyes and mouth and the rest of the face increased the attractiveness of female faces and the opposite was found for male faces. An explanation of these effects is that the contrast between the darker and lighter regions in face is generally larger among women than men. Consequently, increasing the contrast will make a face more feminine while decreasing it will make a face more masculine.

In summary, facial skin plays an important role in facial attractiveness independently of facial shape. Increasing redness and yellowness in faces increases the perceived health and attractiveness of the faces. Homogeneous skin surface is considered more attractive both in male and female faces. Increasing the contrast between the luminance of the darker regions and lighter regions increases the attractiveness of female faces but decreases the attractiveness of male faces.

1.1.5 Eye gaze, head tilt and emotional expressions

While the research discussed above focuses on the influence of physical attributes of faces, such as face shape and skin characteristics, on attractiveness, evidence also suggests the role of social cues in the judgements of facial attractiveness. The social cues that are conveyed in human faces contain important information that facilitates interaction and thus, individuals take these important social cues into consideration, together with the physical attributes, when it comes to the perception of attractiveness.

Eye contact, or gaze, is an important social cue that signals social engagement and influences a range of social evaluations (Kleinke, 1986). Ewing, Rhodes, and Pellicano (2010), using neutral and static female faces as stimuli, showed that female faces with direct gaze were perceived as more attractive than those with averted gaze and were preferred to averted faces. Similarly, Mason, Tatkow, and Macrae (2005), using animations of female faces with neutral expressions as stimuli, revealed that ratings of attractiveness of female faces increased when faces were shifted toward rather than away from male raters. No such effect of shifting was observed for female rates.

While eye contact acts as an efficient signal of one's intention or interests in social interaction, head posture may also function as a social signal, thus affecting facial attractiveness. Indeed, research has shown that slightly downward-tilted female faces are perceived as more attractive than the upward-tilted ones (Burke & Sulikowski, 2010; Osugi & Kawahara, 2015; Sulikowski, Burke, Havlicek & Roberts, 2015). There are two potential explanations for the effect of head tilt on the perceived attractiveness (Sulikowski et al., 2015). One explanation is that downward-tilted female faces were perceived as more attractive because they were perceived more feminine or submissive (Burke & Sulikowski, 2010). Alternatively, the downward-tilted faces appear as though the corners of the mouth are turned upwards, similar to smiling faces, thus increasing attractiveness (Lyons, Campbell, Plante, Coleman, Kamachi, Akamatsu, 2000; Sulikowski et al., 2015). Studies using Japanese participants also replicated this effect of head tilt (Osugi & Kawahara, 2015). They interpreted this bowing effect as downward tilt mimics bowing gesture. The first interpretation is proposed to account for this effect as bowing motion increased the rating of politeness and submissiveness (Osugi & Kawahara, 2015).

Other social cues, such as emotional expression, have been shown to influence attractiveness perception as well. For example, Reis et al. (1990) suggested that individuals were perceived as more attractive when they were smiling than when they were not smiling. Given that expression contains important information of the valence of individuals' emotional states and intentions, integrating the gaze direction and emotional expression would be important for successful interaction and therefore influences the attractiveness perception (Jones, DeBruine, Little, Conway, & Feinberg, 2006). Jones et al. (2006) showed that attractiveness preferences were stronger for smiling faces than for neutral faces in the direct gaze condition, while attractiveness preferences were stronger for neutral faces than smiling faces in the averted gaze condition. Similarly, Conway, Jones, DeBruine, and Little (2008) revealed that people's preferences for faces with direct gaze were stronger when they were judging the attractiveness of happy faces than that of disgusted faces, particularly when they were judging the attractiveness of opposite-sex faces. Collectively, these results suggest that this process may function to facilitate the potential benefits in mating processes.

In summary, both physical attributes of faces such as face shape and skin characteristics and social cues contained in faces such as gaze direction and emotion expression contribute to facial attractiveness.

1.2 Attractive faces are rewarding

The previous part of my introduction has discussed the facial characteristics that contribute to facial attractiveness. Several lines of research have showed that attractive faces are rewarding. The following part will discuss the facial attractiveness in terms of the reward value.

In the following part, I will first introduce the incentive salience theory of reward in general. Next, I will discuss why facial attractiveness can function as a reward. I will then discuss factors that may modulate the reward value of facial attractiveness.

1.2.1 Psychological components of reward

In light of advances in neurobiology, Berridge and Robinson (2003) proposed that reward is not a unitary process but has several different psychological components that mediated by dissociable neural substrates. They have proposed that reward can be parsed into three psychological components: (1) learning, (2) affect or emotion ('liking' and conscious pleasure), and (3) motivation ('wanting' and cognitive wanting). The following will discuss the three components respectively.

1.2.1.1 Learning

Learning the relationships between stimuli and actions is necessary for reward prediction, anticipatory responses, cue guidance and goal-directed action (Berridge & Robinson, 2003). Learning can occur due to either associative or cognitive processes. Associative learning can be either Pavlovian conditioning or instrumental conditioning (Berridge & Robinson, 2003). In Pavlovian conditioning, an association between conditional stimuli (CS, for instance, bell) and unconditional stimuli (UCS, for instance, food) was formed. Consequently, conditional stimuli (e.g., bell) can elicit the conditional response (e.g., salivation) after conditioning (Rescorla, 1967). Conditional stimuli, thus, can elicit responses such as reward anticipatory responses, behavioural habits, conditional motivations and so on. In instrumental conditioning, reinforcement, first proposed by behaviourism, is used to increase specific behavior responses (Skinner, 1963). Behaviour followed by pleasant consequences is likely to be repeated while behaviour followed by unpleasant consequences is likely to stop (Thorndike, 1898). Cognitive learning, however, is more elaborate (Berridge & Robinson, 2003). It involves encoding relationships between stimuli and actions, including understanding the causation between actions and outcomes and reward expectancy.

1.2.1.2 Affect or emotion (‘liking’ and conscious pleasure)

The affect or emotion component is central to reward processing as well. It is essentially a hedonic reaction to the pleasure of a reward (Berridge & Robinson, 2003). The affect or emotion component of reward can be either explicit (i.e., conscious pleasure or liking) or implicit (i.e., hedonic impact, or ‘liking’). Although reward can elicit the subjective experience of conscious pleasure, the underlying core process of hedonic evaluation can exist and control human and animal’s behaviour even in the absence of the subjective states (Berridge & Winkielman, 2003; Berridge, 1999; Berridge & Robinson, 1998, 2003). Following Berridge and Robinson (1998, 2003), the implicit hedonic impact is referred to as ‘liking’ (in quotation marks) and the explicit conscious pleasure as liking (without quotation marks) since the meaning of the word, liking, typically refers to the subjective experience of conscious pleasure.

Berridge and Winkielman (2003) claimed that implicit emotion could affect people’s behaviour without their subjective awareness. For example, unconscious exposure to subliminal happy faces did not change self-reported emotional state but made thirsty participants pour and drink more fruit juice and give higher evaluations of the drinks (Berridge & Winkielman, 2003). In line with this claim, evidence suggests that low doses of the positive reinforcer (e.g. morphine or methamphetamine) could induce addicted behaviour without awareness and apparent subjective hedonic feelings (Hart, Ward, Haney, Foltin, & Fischman, 2001; Lamb et al., 1991).

While the conscious pleasure can be measured by subjective ratings of pleasure, an example of measuring implicit hedonic impact is to measure affective facial expressions (Berridge & Robinson, 2003). Steiner, Glaser, Hawilo, and Berridge (2001) examined affective reactions elicited by tastes from human infants and other infant or adult primates. They found that both sweet and bitter tastes elicited homologous facial affective expressions in humans and other non-human primates (such as chimpanzee and rhesus monkey). Sweet tastes elicit a hedonic pattern of facial expressions such as tongue protrusion while bitter tastes elicit an aversion pattern of reactions such as gape (Steiner et al., 2001).

1.2.1.3 Motivation (incentive salience and cognitive wanting)

The motivation component of reward can be separated from learning and emotion components and yet very important to goal-directed behaviour. Similar to the learning and emotion components, the motivation component includes both explicit cognitive incentives (wanting) and implicit incentive salience (‘wanting’).

The cognitive incentives, according to Berridge and Robinson (2003), are explicit desires. It leads to goal-directed actions and is mediated by neocortical structures, including orbitofrontal and insular cortical regions (Berridge & Robinson, 2003; Dayan & Balleine, 2002). On the other hand, the implicit incentive salience (‘wanting’) is believed to be mediated by a different neural system. The concept of incentive salience was first proposed by Berridge and Robinson (1998) who found that manipulation of dopamine systems affected the motivated behaviour but not hedonic reaction or learning of new hedonic stimulus values. They have argued that incentive salience transforms the brain’s neural representations of a neutral stimulus into an attractive and ‘wanted’ stimulus that individuals will work to acquire. Furthermore, these processes are mediated by dopamine systems and evidence suggests that dopamine systems mediate neither the hedonic impact of a stimulus nor the learning new associative relationships involving hedonic stimuli (Berridge & Robinson, 1998).

While cognitive wanting can be measured by subjective ratings of desire, an example of measuring incentive salience is to measure the efforts required to gain a reward in rats (Dickinson, Smith, & Mirenowicz, 2000; Wyvell & Berridge, 2000, 2001). By using a purely conditioned incentive paradigm, motivational salience can be measured without either primary or secondary reinforcement (Dickinson et al., 2000; Wyvell & Berridge, 2000, 2001). In this paradigm, the rats are first trained to press levers to obtain sucrose pellets and then are conditioned to associate a Pavlovian cue with sucrose pellets. The motivational salience can be tested in the absence of primary reinforcement, e.g., sucrose pellets, and secondary reinforcement by presenting it freely at intervals throughout the session. Recently, the classic lever-press paradigm has been adapted to measure human behaviour (e.g., Aharon et al., 2001), which will be discussed in detail in Session 2.2.4.

1.2.1.4 Emotion and motivation as separate processes

Although rewards usually evoke both emotional and motivational responses, the affect and motivation components of rewards can be dissociable. For instance, Epstein, Truesdale, Wojcik, Paluch, and Raynor (2003) measured the effect of food deprivation on the hedonics and motivational components of food. They found that food deprivation only affected the motivation to eat, but not the hedonic ratings of food. Also, Krishnamurti and Loewenstein (2012) developed scales to assess sexual liking and wanting. Through a confirmatory factor analysis, they claimed that sexual liking and sexual wanting were distinct, measureable, and valid constructs.

In summary, Berridge and Winkielman (2003) propose that reward can be parsed into three separate psychological components: (1) learning, (2) affect, and (3) motivation. The three components are mediated by different neural network and can be measured separately.

1.2.2 Attractive faces as a reward

Both neural and behavioural evidence suggests that viewing attractive faces is rewarding. The following section will review the results of both neural imaging studies and behavioural studies suggesting that attractive faces function as a kind of reward.

1.2.2.1 Neural evidence

In this section, I will first introduce the reward circuitry in human brain. I will then discuss evidence showing that attractive faces evoke activation within the reward circuitry.

Reward circuitry

Using functional Magnetic Resonance Imaging (fMRI), research investigating the neural correlates of face processing suggests that viewing of attractive faces activates reward circuitry (Aharon et al., 2001; Cloutier, Heatherton, Whalen, & Kelley, 2008; Kampe, Frith, Dolan, & Frith, 2001; O'Doherty et al., 2003; Joel S Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007).

The reward circuitry was first proposed by Olds and Milner (1954) who found that electrical stimulation of certain regions of the brain of rats gave the rats pleasure. Subsequent research suggests similar effects of such stimulation on humans (Haber & Knutson, 2010). Reward stimuli activate the human brain extensively, including the prefrontal cortex (i.e. orbital frontal cortex, OFC), basal ganglia (i.e., ventral striatum, dorsal striatum, and amygdala), thalamus, and midbrain dopamine neurons (i.e., ventral tegmental area, VTA) (Haber & Knutson, 2010).

Several lines of research suggest that primary (e.g., food) and secondary rewards (e.g., monetary reward) may activate ventral medial prefrontal cortex (vmPFC) or orbital frontal cortex (OFC) in human brain (Elliott, Friston, & Dolan, 2000; O'Doherty, Critchley, Deichmann, & Dolan, 2003; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001; Thut et al., 1997). Similarly, these rewards increase striatal activity (Elliott et al., 2000; O'Doherty et al., 2003; Small et al., 2001). More specifically, while the nucleus accumbens (NAcc) and medial caudate may respond more strongly to anticipate the reward, the rostroventral putamen may respond more strongly to reward outcomes (Haber & Knutson, 2010). In addition to the striatum, other structures in basal ganglia, such as amygdala plays an important role in reward processing (Murray, 2007; O'Doherty et al., 2003). The amygdala is a part of the limbic system that encodes a broad range of emotional stimuli (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001). Also, the reward circuitry includes the thalamus, which also responds to both primary and secondary rewards (Elliott et al., 2000; Small et al., 2001; Thut et al., 1997).

It is well established that dopamine neurons play a central role in the reward circuit (Berridge & Robinson, 1998; Schultz, 2002; Wise, 2002). Among several dopamine pathways in the brain, the mesolimbic pathway is the most relevant to the reward processing. The mesolimbic pathway arises from the dopamine neurons in ventral tegmental area (VTA) and project to nucleus accumbens (NAcc), amygdala and hippocampus. Although dopamine plays an important role in reward processing, its specific role remains controversial. For instance, some argue that dopamine is important for the pleasure or euphoria of rewards (Wise, Spindler, Dewit, & Gerber, 1978), learning or maintaining habits that lead to rewards (Wise & Schwartz, 1981), or the incentive salience component of rewards (Berridge & Robinson, 1998; Wyvell & Berridge, 2000).

Neural substrates of facial attractiveness

Face stimuli evoke activation within a distributed neural network that includes visual, limbic and prefrontal regions (Hahn & Perrett, 2014; Haxby et al., 2000; Kranz & Ishai, 2006). Haxby et al. (2000) proposed a neural network for face processing that is composed of a “core system” and an “extended system”. The core system is thought to be central to the visual analysis of face stimuli, and includes fusiform gyrus (fusiform face area, FFA), inferior occipital gyri (occipital face area, OFA), and superior temporal sulcus (STS). The extended system is proposed to be crucial to cognitive functions such as spatial attention, speech perception, emotion and biographical information (Haxby et al., 2000). Senior (2003) proposed an additional extended network associated with reward processing. Beautiful faces evoke activation in the sublenticular extended amygdala of the basal forebrain (SLEA) and ventral tegmentum area (VTA), which further project to two separate pathways – the first represents the rewarding component and the second the aesthetic component of faces (Senior, 2003).

Consistent with Senior’s proposal of the extended network associated with reward processing, several lines of research have demonstrated that viewing attractive faces evoke activation of the reward circuitry. For instance, in Aharon et al.'s (2001) study, young heterosexual male participants rated beautiful male and female faces as attractive, but only expended effort (via key-presses) to view attractive female faces. Moreover, neural imaging data showed that passive viewing of beautiful female faces activates men's reward circuitry, including nucleus accumbens (NAcc) and orbitofrontal cortex (OFC, revealed by the Post-Hoc analysis). O'Doherty et al. (2003), using an event-related design, reported that attractive faces evoked activation of the medial orbitofrontal cortex (OFC) but failed to replicate the responses of nucleus accumbens to attractive faces. Other studies reported similar effects of activation in OFC (e.g., Cloutier et al., 2008; Kim, Adolphs, O'Doherty, & Shimojo, 2007; Liang, Zebrowitz, & Zhang, 2010; Joel S. Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007) and NAcc (e.g., Cloutier et al., 2008; Kim et al., 2007; Liang et al., 2010) for attractive faces compared to unattractive faces. Other brain regions known to be relevant to reward processing engage in processing facial attractiveness as well, such as VTA (e.g., Liang et al., 2010), anterior cingulate cortex (e.g., Liang et al., 2010; Joel S. Winston et al., 2007), ventral striatum (e.g., Kampe et al., 2001), prefrontal cortex (such as medial PFC and ventrolateral PFC, Cloutier et al., 2008; O'Doherty et al., 2003) and amygdala (e.g., Liang et al., 2010; Winston et al., 2007).

1.2.2.2 Behavioural evidence

While the neuroimaging studies described above have demonstrated that attractive faces activate the brain area known to be involved in processing other kinds of reward such as food and monetary gain, behavioural studies support the proposal that viewing attractive faces is rewarding as well. For instance, Hayden, Parikh, Deaner, and Platt (2007) investigated whether viewing faces obeyed the same economic principles that guide decisions about rewards. They reported that the reward value of viewing attractive faces was discounted by the delay to viewing, substituted for money and served as an incentive for work (Hayden et al., 2007). Moreover, the reward value of photos of the opposite-sex was modulated by their attractiveness and was greater for men (Hayden et al., 2007). Consistent with this, behavioural evidence suggests that viewing attractive female faces will lead men to discount higher future rewards against smaller immediate rewards (Wilson & Daly, 2004). Collectively, these results suggest that the opportunity to view faces of the opposite-sex follows general economic principles that also applied to other kinds of reward including food and money.

1.2.2.3 Learning, liking and wanting attractive faces

Research discussed above suggests that attractive faces serve as a reward and have all the three psychological components that were proposed by Berridge and Robinson (2003). For the learning component, for instance, participants could learn the association between arbitrary neutral visual stimuli and attractive faces where the attractive faces served as unconditional stimuli in this classical conditioning (Bray & O'Doherty, 2007). They found that after pairing with attractive faces, neutral stimuli were more favoured by participants just like the results for learning with other types of reward (Bray & O'Doherty, 2007).

Attractive faces have the emotional / affective component as well. As for explicit emotions that are evoked by attractive faces, people rated more attractive people as more likeable (Willis & Todorov, 2006). Using facial electromyography to measure facial expression, Principe and Langlois (2011) found that viewing less attractive faces evokes greater disgust and negative affect than more attractive faces. Moreover, neuroimaging evidence suggests that amygdala, a brain region known to encode emotional stimuli, show a non-linear response to facial attractiveness, with greater activation to attractive and unattractive faces compared to those of medium attractiveness (Liang et al., 2010; Winston et al., 2007).

Furthermore, attractive faces have motivational salience. Aharon et al. (2001) used a standard key-press paradigm, similar to the lever-press task used in rodent studies of reward, to assess the motivational salience or ‘wanting’ component of the reward value of facial attractiveness. In this task, participants can control the length of time for which they view faces by repeatedly pressing keys to either increase or decrease the viewing time (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015). In Aharon et al.'s (2001) study, heterosexual male participants rated beautiful male and female faces as attractive, but only expended effort (via key-presses) to view attractive female faces. The dissociation between ratings of attractiveness and key-press scores mirrors the separate processes of ‘liking’ and ‘wanting’ of rewards (Aharon et al., 2001; Berridge & Robinson, 2003). Responses to this type of key-press task are better predictors of neural measures of reward value and motivational salience of face images than attractiveness ratings (Aharon et al., 2001).

In summary, facial attractiveness serves as a kind of reward. Neural imaging evidence shows that attractive faces activate the brain areas known to be involved in processing rewards. Behavioural evidence shows that attractive faces functions as reward as well.

1.2.3 Factors influencing the reward value of attractive faces

Although both neural and behavioral evidence suggest that attractive faces serve as rewards, the reward value of attractive faces is complex. Both facial characteristics of the faces, such as eye direction and emotional expression, and factors of perceivers, such as sex and hormone levels, influence the reward value of faces. This section will review the factors that affect the reward value of faces.

1.2.3.1 Gaze direction

While faces communicate a great deal of information that facilitates social communication (e.g., Adolphs, 2001; Bruce & Young, 1986), eyes are central in social interaction. Studies have shown that gaze functions to provide information, regulate interaction, express intimacy, exercise social control, and facilitate service and task goals (see Kleinke, 1986 for a review).

When encountering an unfamiliar face, eye direction may serve as a social cue of interaction (Kampe et al., 2001). In Kampe et al. (2001), participants viewed faces with eye gaze either directed at or averted from participants during an fMRI scanning session and they rated the attractiveness of the faces after scanning. They found that when eye gaze was directed at the participants, responses in the ventral striatum were positively related to attractiveness ratings. In contrast, when eye gaze was averted, the activation in the ventral striatum was negatively related to attractiveness ratings (Kampe et al., 2001). Given that ventral striatum is thought to be involved in reward processing (e.g., Schultz, 1998), this pattern of results revealed that returned eye gaze from a more attractive face is more rewarding than that from a less attractive face while averted gaze from a more attractive face is more disappointing than that from an unattractive face (Kampe et al., 2001). These results suggest that the reward value of attractive faces is modulated by social cues such as gaze direction.

1.2.3.2 Facial expression

In addition to gaze direction, emotional expressions are important social signals that are central in social interactions as well. For example, negative facial expressions, such as anger, elicit avoidance-related behaviours (Marsh, Ambady, & Kleck, 2005) while positive facial expressions, such as smiling, encourage approach-related behaviours (Miles, 2009).

As a result, facial expression could also modulate the reward value of facial attractiveness (Jaensch et al., 2014; O'Doherty et al., 2003). For instance, the activation in the orbitofrontal cortex is more pronounced in response to attractive faces than unattractiveness faces. Moreover, this effect is qualified by an interaction between attractiveness and happiness, which suggests that the reward value of facial attractiveness is more pronounced for faces with smiling facial expression (O'Doherty et al., 2003).

Negative facial expressions such as anger, on the other hand, discount the reward value of attractive faces (Jaensch et al., 2014). Jaensch et al's (2014) used a standard key-press task (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015) to assess the reward value of images of female faces in male participants, which is believed to be a better predictor of neural measures of the reward value and motivational salience of face images than attractiveness ratings (Aharon et al., 2001). They found that male participants key-pressed to extend the viewing time for happy and neutral attractive faces but to reduce the viewing time for attractive angry faces. Although angry attractive faces were rated as more attractive than unattractive faces, male participants worked to reduce the viewing time for angry attractive faces to an extent comparable with unattractive neutral and happy faces (Jaensch et al., 2014). In addition, male participants key-pressed to reduce the viewing time of unattractive faces, with no differences in viewing time for happy, angry or neutral expressions.

1.2.3.3 Sex differences

Although it is commonly believed that attractiveness judgements are generally universal across sexes, it is less clear that whether men and women respond differently to facial attractiveness in terms of reward value.

There is at least some evidence to support the proposal that people value the facial attractiveness of their preferred-sex faces more than that of the non-preferred sex. For instance, Aharon et al. (2001) showed that heterosexual male participants only worked harder to extend the viewing time of attractive female faces than same-sex faces while rated the attractiveness similarly for both male and female faces. Neuroimaging results also showed that attractive female faces activated stronger responses in reward circuitry, particularly nucleus accumbens (Aharon et al., 2001). Instead of testing only heterosexual male participants (Aharon et al., 2001), Kranz and Ishai (2006) investigated potential sex and sexual orientation effects of the neural responses to faces. They found that activations in the thalamus and medial orbitofrontal cortex were stronger for preferred-sex than non-preferred sex faces, suggesting a preferred-sex bias to the reward value of facial attractiveness. Similarly, evidence from behavioural studies using the key-pressed task to assess the motivational salience of facial attractiveness also suggests a preferred-sex bias (Hahn, Fisher, DeBruine, & Jones, 2015).

While the studies described above suggest a preferred-sex bias in response to the motivational salience of facial attractiveness, other studies suggested the sex differences in responses to the motivational salience of facial attractiveness. For instance, behavioural studies showed that heterosexual men worked harder to extend the viewing time of female face than women to view male faces (Hahn, Xiao, Sprengelmeyer, & Perrett, 2013; Levy et al., 2008). Similarly, there are neuroimaging studies suggesting the similar pattern of results. For instance, Cloutier et al. (2008) reported sex differences in activations in orbitofrontal cortex in response to facial attractiveness of opposite-sex faces. Winston et al. (2007) reported similar sex differences in anterior cingulate, which distinguished attractive and unattractive faces only for male participants.

However, many studies failed to find any opposite-sex bias or sex differences in response to facial attractiveness (e.g., Kampe et al., 2001; Liang et al., 2010). Moreover, instead of suggesting a general male bias for opposite-sex faces, Spreckelmeyer, Rademacher, Paulus, and Gruender (2013) proposed that men and women recruited different brain regions in processing the reward value of facial stimuli. By using a social incentive delay task, they found that while some brain regions, such as ventral tegmental area and superior temporal gyrus, showed stronger activation to opposite-sex faces among women than among men, other regions, such as nucleus accumbens, showed the opposite pattern of results (Spreckelmeyer et al., 2013).

1.2.3.4 Possible effect of women's hormone levels

Women's hormone levels have been found to modulate neural activity in response to monetary reward (Dreher et al., 2007; Hermans et al., 2010). Evidence has shown that women's reward circuitry is more active during the follicular phase than the luteal phase, both at the reward anticipation and reward delivery phase (Dreher et al., 2007). Moreover, the activity of the reward system in women peaked at the midfollicular phase when estrogen is unopposed by progesterone. Further analysis revealed that women's estradiol level was positively related to the activations in amygdalo-hippocampal complex (Dreher et al., 2007). In addition, Hermans et al. (2010) demonstrated that administrating testosterone to women increased activation in ventral striatum during reward anticipation, especially among women with low intrinsic appetitive motivation.

Given the studies mentioned above suggesting that women's hormone levels modulate the neural activation in response to monetary reward, it is possible that hormone levels also influence how women process the reward value of facial attractiveness. Consistent with this proposal, Rupp et al. (2009) investigated the effect of menstrual cycle on the neural activation to male faces. Results demonstrated that activation in medial orbitofrontal cortex (OFC) increased during follicular phase compared to luteal phase. Further analysis showed that activation in OFC was positively correlated with women's estradiol to progesterone ratios (Rupp et al., 2009).

In summary, social cues that express the positive interests of interaction enhance the reward value of facial attractiveness while negative social cues discount the reward value of facial attractiveness. Both the sex of observer and the sex of face may modulate the reward value of facial attractiveness. In addition, women's hormone levels also module the reward value of facial attractiveness.

1.3 Facial attractiveness and memory for face photographs

Recognising faces of people whom we are supposed to know is important for successful social interaction. It is an essential skill that most of us gain without additional training. In this section, I will first introduce the cognitive model proposed to explain the processes involved in recognising faces. Next, I will discuss the research investigating the facial characteristics that may affect memory for face photographs. Facial attractiveness is known to affect memory for face photographs as well. The effect of physical attractiveness on memory for face photographs will be discussed at the end.

1.3.1 Cognitive model of face recognition

How do people recognise faces? The model proposed by Bruce and Young (1986) is probably the most influential one of face recognition. According to their proposal, the process of face recognition starts with structural encoding, which includes view-centered descriptions and expression-independent descriptions. These can be descriptions of global configuration or features of the face that provide input for analysis of expression and facial speech. Next, the face representation will be transformed from view-centered descriptions to abstract view-independent descriptions, which will then be compared with stored representations of known faces in the face recognition units (FRUs). If it matches to any stored representation, it can be referred as a known face and will be entered into next stage, the person identity nodes (PINs). When the person identity node is activated, the associated identity information will be retrieved. Finally, the name generation unit will be activated and the name of the face can be retrieved.

Interestingly, there are remarkable differences between recognising a familiar and an unfamiliar face. While recognising familiar faces can rely on more reliable facial cues such as facial shape, the recognition of unfamiliar faces can be easily disrupted by changeable cues, such as a different angle (Bruce, Valentine, & Baddeley, 1987). People use pictorial codes to encode unfamiliar faces, which means people rely more heavily on information related to the entire image, rather than information only related to the face itself, to encode the faces (Bruce & Young, 1986). In the face recognition model proposed by Bruce and Young (1986), the view-centred descriptions generated in the first stage can be used to complete old-new memory tasks or an eyewitness memory task. Because of the pictorial coding based on external cues, the memory of unfamiliar faces can be vulnerable to any changes in external cues, such as lighting, viewpoint, and expression (Young & Bruce, 2011).

1.3.2 Typicality, distinctiveness and memory for faces photographs

Much research has examined the facial characteristics that affect memorability of face photographs. Research into the characteristics that predict the performance of face recognition traditionally emphasises the importance of facial typicality / distinctiveness.

Early research has demonstrated the effect of facial typicality / distinctiveness on face memory tasks (Light, Kayrastuart, & Hollander, 1979; Shepherd, Gibling, & Ellis, 1991; Valentine, 1991). More specifically, distinctive faces as targets are more easily to be recognised than typical faces (Shepherd et al., 1991; Valentine, 1991); distinctive faces as distractors are less likely to be falsely recognised than typical faces (Light et al., 1979; Valentine, 1991). Although there are consistent results on the effect of typicality / distinctiveness on memorability of face photographs, there are different ways that researchers measure the typicality / distinctiveness of faces. For instance, Valentine (1991) instructed participants to "imagine that they had to meet each person at a railway station and to rate each face for how easy it would be to spot in a crowd". A face that is easy to spot in a crowd is considered to be distinctive (7=very distinctive) and on the contrary, a face difficult to identify in a crowd is typical (1=very typical). Wickham and Morris (2003), however, instructed participants to rate typicality based on the extent to which the presented faces deviated from other faces that they know (1=very typical to 7=very atypical). Others instructed to rate typicality or distinctiveness without further definition (e.g., Shepherd et al., 1991). There is some evidence to suggest that although different measurements have different distributions, all of the distinctiveness measures predicted the recognition memory of face photographs (Wickham, Morris, & Fritz, 2000).

Theories were proposed to explain the influence of distinctiveness on memory for faces. For instance, Valentine (1991) developed a multidimensional space framework to represent faces in which different aspects of faces will be represented in different dimensions. It is assumed that typical faces are close to central tendency while distinctive faces are far away from central tendency. Accordingly, distinctive faces can be identified more accurately and rapidly than typical ones because there will be fewer faces nearby to confuse the matching process. Similarly, a distinctive new face can be rejected more accurately and rapidly because the representation of the new face will be located in regions with low density and therefore it is less likely that a stored face will be close enough to confuse the match (Valentine, 1991). Other researchers, Vokey and Read (1992) for instance, suggest that the effect of typicality on recognition is a function of rated familiarity and rated memorability.

In summary, traditional research into the characteristics that predict the performance of face recognition emphasises the importance of distinctiveness / typicality. Distinctive faces are associated with better performance of face memory task than typical faces.

1.3.3 Attractiveness and memory for face photographs

Previous research has suggested the existence of adaptations for mate choice in human memory (Allan, Jones, DeBruine, & Smith, 2012). Moreover, many studies also suggest that facial attractiveness influences recognition memory for face photographs.

Although a number of studies have been conducted to investigate this issue, no consensus has been reached on the relationship between facial attractiveness and memory performance for faces. While some studies suggested that perceived facial attractiveness is associated with better recognition performance (Cross, Cross, and Daly, 1971; Marzi and Viggiano, 2010), other studies revealed the opposite pattern of results (Light, Hollander, and Kayra-Stuart, 1981; Sarno & Alley, 1997; Wiese, Altmann, & Schweinberger, 2014) or no significant relationships betweeen facial attractiveness and memory for face photographs (e.g., Wickham & Morris, 2003).

One possible explanation for the mixed pattern of results might be the confounding effect of other facial characteristics that might also contribute to memorability of faces. For instance, as mentioned in the previous section, distinctiveness is proposed to affect memory for faces (Valentine, 1991). After controlling the effect of distinctiveness, Wiese et al. (2014) found that attractive faces were harder to remember. Similarly, Bainbridge, Isola, and Oliva (2013) revealed a similar pattern of results when controlling for other facial characteristics that might also contribute to memory for face photographs.

In summary, early research investigating the relationships between facial attractiveness and memory for photographs reveals inconsistent patterns of results. However, more recent work suggests that more attractive faces tend to be less memorable.

1.4 Current research

In this thesis, I will first investigate within-woman variability in the motivational salience of facial attractiveness (Chapter 2). Next, I will examine whether physical characteristics other than attractiveness contributes to the motivational salience of facial attractiveness (Chapter 3). Chapter 4 will investigate between-women variability in the effects of attractiveness on the motivational salience of faces and memory for faces. Finally, I will investigate the perceptual components underlying the memorability of face photographs (Chapter 5).

In Chapter 2, I test the possible effects of women's salivary hormone levels (estradiol, progesterone, testosterone, and estradiol-to-progesterone ratio) on the motivational salience of facial attractiveness. Although there is evidence for hormonal modulation on women's face preferences (see Gildersleeve, Haselton, & Fales, 2014 for a meta-analytic review), these results are controversial (Gildersleeve et al., 2014). Furthermore, no previous research has investigated whether hormone levels modulate the motivational salience of facial attractiveness. I investigate this issue using a standard key-press task to assess the motivational salience of images of men's and women's faces among women participants and a longitudinal design in which each woman provided a saliva sample and completed the key-press task in five weekly test sessions. The results suggest that physically attractive faces generally have greater motivational salience than relatively unattractive faces and that the motivational salience of facial attractiveness is greatest when women's testosterone levels are high.

In Chapter 3, I investigate whether facial dominance also contributes to the motivational salience of faces. Chapter 2's results suggest that the motivational salience of faces is positively correlated with their physical attractiveness, a pattern of results reported in previous studies too (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015). Whether characteristics other than attractiveness contribute to the motivational salience of human faces is unclear, however. Research with male macaques has previously shown that more dominant macaques' faces hold greater motivational salience (Deaner, Khera, & Platt, 2005). Consequently, in this chapter I investigate whether facial dominance also contributes to the motivational salience of faces in human participants. First, I had the faces rated for a diverse range of traits. Principal component analysis of the ratings for these traits revealed two orthogonal components (valence and dominance). The first component ("valence") is highly correlated with rated trustworthiness and attractiveness. The second component ("dominance") is highly correlated with rated dominance and aggressiveness. Both valence and dominance components are positively and independently related to the motivational salience of faces.

While Chapter 2 investigates the within-woman differences in the motivational salience of facial attractiveness and Chapter 3 investigates general responses to facial cues, Chapter 4 will investigate between-women variability in response to male attractiveness. Some researchers have proposed that partnered individuals discriminate opposite-sex individuals less along the physical attractiveness dimension than do unpartnered individuals (Karremans, Dotsch, & Corneille, 2011; Ritter, Karremans, & van Schie, 2010). This pattern of results is thought to protect romantic relationships by decreasing the appeal of attractive alternative mates (Karremans et al., 2011; Ritter et al., 2010). In Chapter 4, I test for further evidence of this by comparing the effects of men's attractiveness on partnered and unpartnered women's performance on two measures for which attractiveness is known to be important: memory for face photographs (Study 1) and the motivational salience of faces (Study 2). Consistent with previous research, these studies suggest that women's memory is poorer for face photographs of more attractive men (Study 1) and that the motivational salience of faces is more pronounced for more attractive men's faces (Study 2). However, in neither study were these effects of attractiveness modulated by women's partnership status. Among partnered women, commitment to and happiness with their romantic relationships also did not modulate the effects of attractiveness.

A key result from Chapter 4 is that more attractive faces were harder to remember. Building on this result, Chapter 5 investigates the characteristics that contribute to the memorability of face photographs. Research suggested that many different traits contribute to the memorability of face photographs. What components underlie these traits is unclear, however, as is how these components relate to the actual memorability of face photographs. Principal component analysis of third-party ratings of faces for multiple traits in Chapter 5 reveals three orthogonal components that are highly correlated with trustworthiness, dominance, and memorability ratings, respectively. Importantly, each of these orthogonal components also predicts the actual memorability of face photographs.

For all the studies presented in this thesis, participants provided informed written consent before participating and University of Glasgow's School of Psychology Ethics Committee had approved all aspects of the study.

Chapter 2

Women's hormone levels modulate the motivational salience of facial attractiveness

The following chapter is based on work published in Psychoneuroendocrinology.

Wang, H., Hahn, A. C., Fisher, C. I., DeBruine, L. M., & Jones, B. C. (2014). Women's hormone levels modulate the motivational salience of facial attractiveness and sexual dimorphism. *Psychoneuroendocrinology*, 50, 246-251.

Abstract

The physical attractiveness of faces is positively correlated with both behavioral and neural measures of their motivational salience. Although previous work suggests that hormone levels modulate women’s perceptions of others’ facial attractiveness, studies have not yet investigated whether hormone levels also modulate the motivational salience of facial characteristics. To address this issue, we investigated the relationships between within-subject changes in women’s salivary hormone levels (estradiol, progesterone, testosterone, and estradiol-to-progesterone ratio) and within-subject changes in the motivational salience of attractiveness in male and female faces. Physically attractive faces generally hold greater motivational salience, replicating results from previous studies. Importantly, however, the effect of attractiveness on the motivational salience of faces was greater in test sessions where women had high testosterone levels. Additionally, the motivational salience of attractive female faces was greater in test sessions where women had high estradiol-to-progesterone ratios. These results provide the first evidence that the motivational salience of facial attractiveness is modulated by within-woman changes in hormone levels.

2.1 Introduction

Facial attractiveness is a particularly salient social cue that influences many important social outcomes. For example, people prefer to mate with, date, associate with, hire, and vote for attractive individuals (see Langlois et al., 2000 for a meta-analytic review). Several lines of evidence also demonstrate that physically attractive faces have motivational salience. For example, the extent to which people will key press to increase the length of time for which they can view faces is correlated with the physical attractiveness of the faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013). Additionally, compared to viewing physically unattractive faces, viewing physically attractive faces elicits greater activation in brain regions implicated in motivation and the processing of rewards, such as the nucleus accumbens and medial orbitofrontal cortex (see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013 for meta-analytic reviews). Moreover, behavioral measures of motivational salience predict neural measures of faces' reward value better than do perceptions of attractiveness measured by ratings (Aharon et al., 2001).

Several lines of evidence suggest that changes in women's hormone levels during the menstrual cycle may affect their perceptions of others' facial attractiveness (see Gildersleeve et al., 2014 for a meta-analytic review). For example, studies have reported that women's preferences for masculine men are positively correlated with their estradiol (e.g., Roney & Simmons, 2008; Roney et al., 2011) or testosterone (e.g., Welling et al., 2007; Bobst et al., 2014) levels. By contrast with the relatively large number of studies investigating how women's *perceptions* of others' attractiveness covary with changes in women's hormone levels, no previous studies have tested for effects of women's hormone levels on the *motivational salience* of facial attractiveness. This is surprising, given the importance of attractiveness for social interaction (Langlois et al., 2000) and research suggesting that women's testosterone (Hermans et al., 2010) or estradiol (Dreher et al., 2007) modulates the extent to which financial incentives activate brain regions involved in motivation and the processing of reward.

In light of the above, we investigated the hormonal correlates of within-woman changes in the motivational salience of male and female facial attractiveness. Women (none of whom were using any form of hormonal supplement, such as hormonal contraceptives) were each tested once a week for five weeks (i.e., each woman completed five weekly test sessions). In each of these test sessions, the motivational salience of male and female facial attractiveness was assessed and a saliva sample was collected. The motivational salience of faces was measured using a standard key-press task that has previously been shown to be a particularly good predictor of neural measures of the reward value of faces (Aharon et al., 2001). Saliva samples were analyzed for estradiol, progesterone, and testosterone levels.

2.2 Methods

2.2.1 Participants

Fifty heterosexual women (mean age=21.2 years, SD=2.89 years) participated in the study. All participants were students at the University of Glasgow (Scotland, UK). None of these women were currently pregnant, breastfeeding, or taking any form of hormonal supplement, and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation.

2.2.2 Face stimuli

Stimuli were full-color face images of 50 white adult men (mean age=24.2 years, SD=3.99 years) and 50 white adult women (mean age=24.3 years, SD=4.01 years). Photographs were taken under standardized photographic conditions and depicted individuals who were posed front on to the camera with neutral emotional expressions and direct gaze. Images were aligned on pupil position and masked so that clothing was not visible. Figure 2.1 shows examples of male and female face images used in the study.

Figure 2.1 Examples of male and female faces used in the study

In order to establish the attractiveness of the faces for comparison with motivational salience, the 50 male faces were rated for attractiveness by 100 heterosexual women and 100 heterosexual men (mean age=24.7 years, SD=5.87 years) using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. A different set of 100 heterosexual women and 100 heterosexual men (mean age=25.0 years, SD=5.56 years) rated the 50 female faces using the same 7-point scale. Participants were randomly allocated to rate either male or female faces. Trial order within each block was fully randomized.

Inter-rater agreement was high for attractiveness ratings of both the male (Cronbach's α=.99) and female (Cronbach's α=.99) faces. Because mean ratings derived from female and male raters' scores were highly correlated for both male (r=.97, N=50, p<.001) and female (r=.96, N=50, p<.001) faces, we combined ratings from female and male raters to produce a single attractiveness score for each face. These facial attractiveness scores were used in our main analyses (see section 2.3 Results).

2.2.3 Procedures

In order to investigate how hormone levels might modulate the motivational salience of faces, each of the 50 women in our main study completed five weekly test sessions. During each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Each woman's test sessions took place at the same time of day to control for possible effects of diurnal changes in hormone levels (Veldhuis et al., 1988; Bao et al., 2003).

In each test session, participants completed two versions of a standard key-press task, similar to those used to assess the motivational salience of faces in previous studies (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013). Following Aharon et al. (2001) and Levy et al. (2008), and because the faces had been rated in single-sex blocks (see section 2.2.2), male and female faces were presented in separate blocks of trials. In one version of the task (male face version), the 50 male faces described in section 2.2.2 were presented in a fully randomized order. In the other version of the task (female face version), the 50 female faces described in section 2.2.2 were presented, again in a fully randomized order. Within each test session, participants completed the male face version of the task and the female face version in a random order.

In each version of the key-press task, participants controlled the viewing duration of each face image by repeatedly pressing designated keys on their keyboard after initiating each trial by pressing the space bar. Participants could increase the length of time a given face was displayed by alternately pressing the 7 and 8 keys and/or decrease the length of time a given face was displayed by alternately pressing the 1 and 2 keys. Each key press increased or decreased the viewing duration by 100ms. The default viewing duration for each image (i.e., the length of time a face remained onscreen if no keys were pressed) was 4 seconds. Participants were told that the key-press task would last for a total of 3.5 minutes in order to discourage responses aimed at changing the length of engagement with the task. However, in reality, the total length of the key-press task was dependent on participants' responses. All participants key-pressed at least once in each version of the task in all test sessions. Participants completed a block of practice trials at the start of each test session to ensure they understood the task (face images were not shown in this block of practice trials).

Following previous studies of the motivational salience of faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013), key-press scores for each face were calculated by subtracting the number of key presses made to decrease viewing time from those made to increase viewing time. These scores were calculated separately for each participant and for each test session and served as the dependent variable in our analyses (see section 2.3). Faces with greater key press scores are those with greater motivational salience (Aharon et al., 2001).

2.2.4 Hormonal assays

Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis. Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, drinking, chewing gum or brushing their teeth in the 60 minutes prior to participation. Samples were assayed by Salimetrics using the Salivary 17β-Estradiol Enzyme Immunoassay Kit 1-3702 (M=4.27 pg/mL, SD=1.07 pg/mL), Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=148.82 pg/mL, SD=65.63 pg/mL), and Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (M=82.99 pg/mL, SD=21.25 pg/mL). All assays passed Salimetrics' quality control. Estradiol, progesterone, and testosterone were assayed because changes in these hormones have been implicated in studies of within-woman changes in perceptual judgments of faces (reviewed in Roney et al., 2011). We also calculated estradiol-to-progesterone ratio ($M=0.03$, $SD=0.02$) from women's estradiol and progesterone data because estradiol-to-progesterone ratio is correlated with fertility (Landgren et al., 1980; Baird et al., 1991) and some researchers have suggested that women's responses to facial cues may covary with estrogen-to-progesterone ratio (e.g., Frost, 1994).

2.3 Results

Multilevel analyses with cross-classified structures were used to test for within-subject effects of hormone levels on the motivational salience of faces. All continuous predictors were centered on their grand means. Key-press scores served as our dependent variable in our analyses and analyses were conducted using R (R Core Team, 2013), lme4 (Bates et al., 2014), and lmerTest (Kuznetsova et al., 2013). Random effects of session nested within participant, face and the interaction between participant and face were included. The equations and full results for each model are given in the Supplemental materials.

Testosterone, estradiol, progesterone, and estradiol-to-progesterone ratio were entered for each participant's test session to test for independent within-subject effects of the different hormone measures on key-press scores. Facial attractiveness and sex of face (0 = female, 1 = male) were entered for each face (see the section 2.2 for details of these ratings). Interactions between facial attractiveness and each of the hormone measures, between sex of face and each of the hormone measures, between facial attractiveness and sex of face, and among facial attractiveness, sex of face and each of the hormone measures were also included in our initial model.

This initial analysis revealed no three-way interactions among facial attractiveness, sex of face and any of the hormone measures (all $|t| < 1.30$, all $p > .19$), except for estradiol-to-progesterone ratio ($t = -2.22$, $p = .027$). There were no significant two-way interactions between sex of face and any of the hormone measures or facial attractiveness (all $|t| < 1.57$, all $p > .11$). The effect of facial attractiveness interacted with testosterone ($t = 5.71$, $p < .001$) and estradiol-to-progesterone ratio ($t = 2.43$, $p = .015$), but not estradiol or progesterone (both $|t| < 0.82$, both $p > .41$).

To interpret these results, all non-significant interactions were removed from the model. There was a significant positive effect of testosterone (t = 2.39, p = .018), indicating that key-press scores were generally greater in test sessions with higher testosterone levels. These effects were qualified by the significant interaction between facial attractiveness and testosterone (t = 6.66, p < .001), indicating that the positive effect of facial attractiveness on key-press scores was more pronounced in test sessions with higher testosterone levels (see Figure 2.1). Note that our initial model showed no significant three-way interaction among sex of face, facial attractiveness, and testosterone.

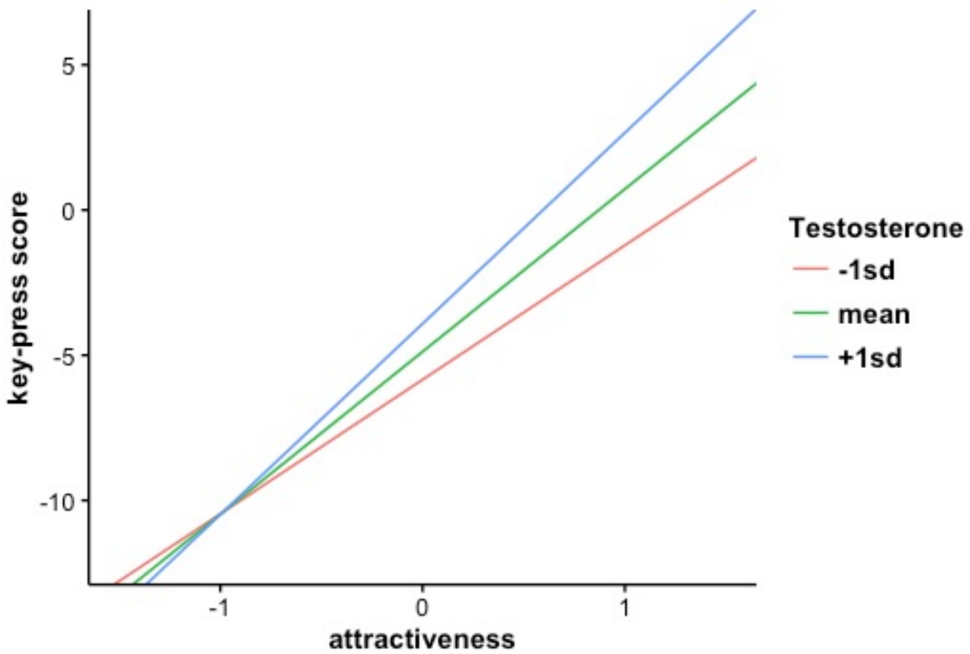

Figure 2.2 Interaction between facial attractiveness and testosterone on key-press scores. The red, green, and blue lines represent the effect of facial attractiveness on key-press scores when testosterone levels are 1sd below the mean, mean, and 1sd above the mean respectively.

The three-way interaction among facial attractiveness, sex of face, and estradiol-to-progesterone ratio was significant in this reduced model (t = -2.75, p = .006). For female faces, there was a significant positive effect of facial attractiveness (t = 9.43, p < .001), confirming that more attractive female faces generally had greater motivational salience, and no effect of estradiol-to-progesterone ratio (t = -0.14, p = .89). However, the effect of female facial attractiveness on key-press scores was greater in test sessions with higher estradiol-to-progesterone ratio (t = 3.31, p < .001, see Figure 2.3). For male faces, there was also a significant positive effect of facial attractiveness ($t = 10.72$, $p < .001$), and the effect of estradiol-to-progesterone ratio was not significant ($t = 0.52$, $p = .60$). By contrast with our results for female faces, the effect of male facial attractiveness on key-press scores did not vary as a function of estradiol-to-progesterone ratio ($t = -0.70$, $p = .48$, see Figure 2.4).

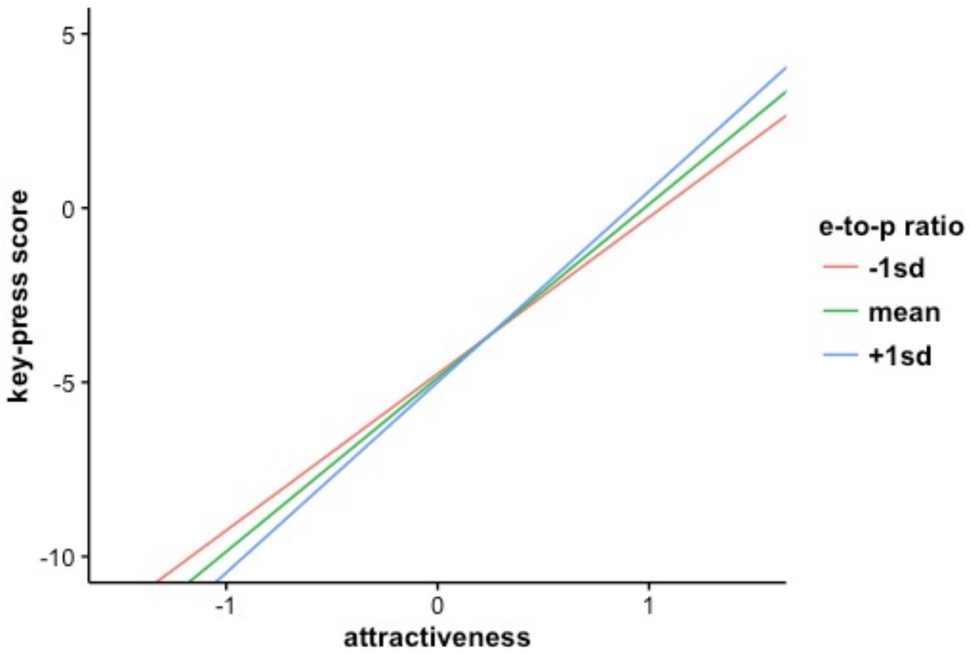

Figure 2.3 Interaction between facial attractiveness and testosterone on key-press scores for female faces. The red, green, and blue lines represent the effect of facial attractiveness on key-press scores when estradiol-to-progesterone ratios are 1sd below the mean, mean, and 1sd above the mean respectively

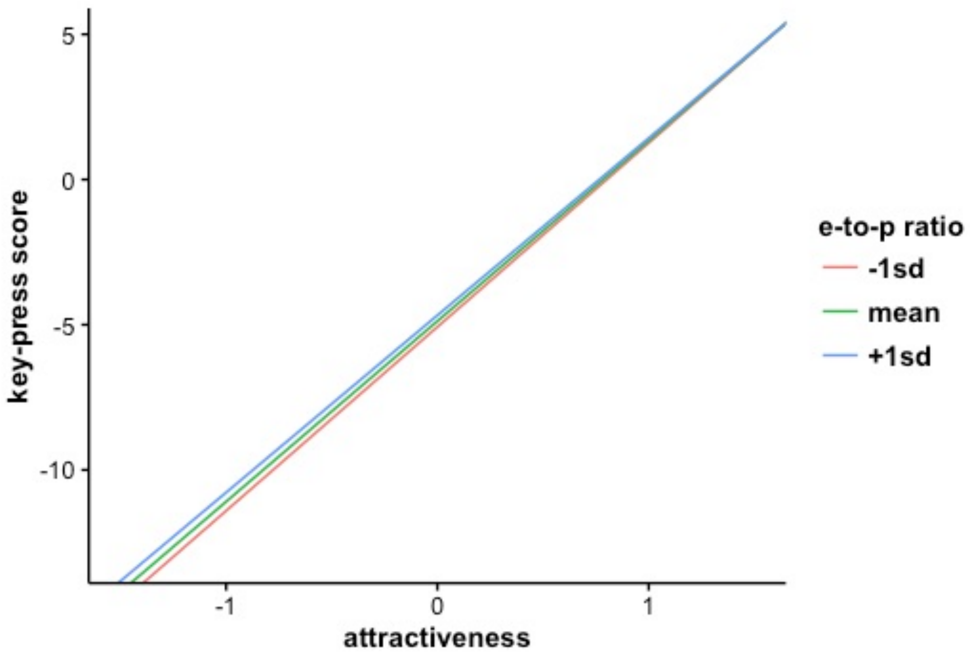

Figure 2.4 Interaction between facial attractiveness and testosterone on key-press scores for male faces. The red, green, and blue lines represent the effect of facial attractiveness on key-press scores when estradiol-to-progesterone ratios are 1sd below the mean, mean, and 1sd above the mean respectively

2.4 Discussion

Consistent with the results of previous behavioral (e.g., Hahn et al., 2013) and neuroimaging (see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013 for meta-analytic reviews) studies, physically attractive male and female faces generally had greater motivational salience than relatively unattractive faces. However, our analyses also suggested that the motivational salience of facial attractiveness was modulated by changes in women's hormone levels.

The effect of physical attractiveness on the motivational salience of faces interacted with the effect of women’s salivary testosterone level. Furthermore, this interaction was not qualified by a higher-order interaction involving sex of face, suggesting that testosterone has similar effects on the motivational salience of attractiveness for male and female faces. Attractiveness had greater positive effects on the motivational salience of faces in test sessions where women had higher salivary testosterone levels. Our results then suggest that women’s testosterone levels modulate the motivational salience of facial attractiveness, consistent with the results of studies in which administering testosterone to women increased responses to financial incentives in brain regions implicated in motivation and reward processing (Hermans et al., 2010). Consequently, our data present new, converging evidence that testosterone plays a potentially important role in reward sensitivity (McCall & Singer, 2012). Some prior work suggests that viewing faces *in general* is rewarding (e.g., Kawabata & Zeki, 2008). This being the case, that we found the motivational salience of faces *in general* to be greater when testosterone levels were high also supports McCall and Singer's (2012) proposal.

The effect of physical attractiveness on the motivational salience of female faces, but not male faces, was greater in test sessions with high estradiol-to-progesterone ratios and this effect of estradiol-to-progesterone ratio on the motivational salience of female facial attractiveness was independent of the effects of testosterone level. Given strong associations between estradiol-to-progesterone ratio and conception risk (Landgren et al., 1980; Baird et al., 1991), these results suggest that women may be more sensitive to female attractiveness at this time. That attractive female faces have greater motivational salience to women when their estradiol-to-progesterone ratio is high is, perhaps, surprising, given that some previous research has suggested that women derogate the attractiveness of other women when conception risk is high (Fisher, 2004). That attractive female faces have greater motivational salience to women when their estradiol-to-progesterone ratio is high suggests that women do not necessarily increase avoidance of attractive competitors for mates when conception risk is high. We speculate here that greater motivational salience for attractive female faces when estradiol-to-progesterone ratio is high may function to facilitate enhanced monitoring of attractive competitors and/or modeling of those competitors' behaviors at points in the menstrual cycle when women are thought to be more likely to compete for high-quality mates (Fisher, 2004). Estradiol-to-progesterone ratio and testosterone may have different effects on responses to male faces because, while estradiol-to-progesterone ratio is a very good predictor of conception risk across the menstrual cycle (Landgren et al., 1980; Baird et al., 1991), testosterone may be more sensitive to situational factors related to competition for resources and mating (van Anders et al., 2011).

In conclusion, our analyses of salivary hormone levels suggest that the motivational salience of facial attractiveness is modulated by within-woman changes in testosterone levels and, to a lesser extent, estradiol-to-progesterone ratios. Previous studies have demonstrated that the motivational salience of attractive faces is variable by showing that other types of facial cue (e.g., emotional expression or gaze direction) can modulate responses to physically attractive versus physically unattractive faces in brain regions involved in motivation and reward processing (Kampe et al., 2001; O'Doherty et al., 2003). Here we present new evidence that the motivational salience of physically attractive faces is variable, finding that within-woman changes in hormone levels also modulate the motivational salience of physically attractive faces. Moreover, these changes in the reward value of facial attractiveness may contribute to changes in women's actual behaviour towards physically attractive and unattractive individuals during the menstrual cycle (e.g., Senior et al., 2007; Lucas & Koff, 2013). However, we note here that although within-woman changes in hormone levels might contribute to women's behaviour changes towards physically attractive and unattractive individuals, this effect might be smaller and less robust compared to between-women effects (Havlíček, Cobey, Barrett, Klapilova, & Roberts, 2015).

The results of this study suggest that the motivational salience of faces is positively correlated with their physical attractiveness, a pattern of results reported in previous studies too (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015). The next chapter will investigate whether characteristics other than attractiveness contribute to the motivational salience of faces.

Chapter 3

The motivational salience of faces is related to both their valence and dominance

The following chapter is based on work published in PLoS ONE.

Wang, H., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2016). The Motivational salience of faces is related to both their valence and dominance. *PLoS ONE,* 11(8):e0161114. DOI: 10.1371/journal.pone.0161114

Abstract

Both behavioural and neural measures of the motivational salience of faces are positively correlated with their physical attractiveness. Whether physical characteristics other than attractiveness contribute to the motivational salience of faces is not known, however. Research with male macaques recently showed that more dominant macaques' faces hold greater motivational salience. Here we investigated whether dominance also contributes to the motivational salience of faces in human participants. Principal component analysis of third-party ratings of faces for multiple traits revealed two orthogonal components. The first component ("valence") was highly correlated with rated trustworthiness and attractiveness. The second component ("dominance") was highly correlated with rated dominance and aggressiveness. Importantly, both components were positively and independently related to the motivational salience of faces, as assessed from responses on a standard key-press task. These results show that at least two dissociable components underpin the motivational salience of faces in humans and present new evidence for similarities in how humans and non-human primates respond to facial cues of dominance.

3.1 Introduction

Multiple lines of evidence suggest that viewing attractive faces is rewarding (for reviews see Bzdok et al., 2011; Hahn & Perrett, 2014; Mende-Siedlecki et al., 2013).

For example, brain regions involved in the general processing of rewards, such as the nucleus accumbens and orbitofrontal cortex (see Haber & Knutson, 2010 for a review), respond more strongly when viewing physically attractive faces than they do when viewing physically unattractive faces (see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013 for meta-analytic reveiws). Consistent with these results, studies that have used key-press tasks to assess the motivational salience of faces (i.e., the extent to which participants will expend effort to alter the viewing time for a face) have reported that participants are willing to expend more effort to look longer at more attractive faces (Aharon et al., 2001; Levy et al., 2008; Hahn, Fisher, DeBruine, & Jones, 2015; Wang, Hahn, Fisher, DeBruine, & Jones, 2014). Some studies of heterosexual participants have reported that this effect of attractiveness on the motivational salience of faces tends to be greater when viewing opposite-sex than own-sex faces (e.g., Hahn et al., 2015; Hahn, Xiao, Sprengelmeyer, & Perrett, 2013), while others have reported this opposite-sex bias for male, but not female, participants (e.g., Levy et al., 2008) or have not observed an opposite-sex bias (e.g., Wang et al., 2014).

Whether physical characteristics other than attractiveness contribute to the motivational salience of faces is currently an unresolved issue. However, male macaques will exchange rewards in order to view dominant conspecifics' faces, suggesting that more dominant-looking faces hold greater motivational salience for male macaques (Deaner, Khera, & Platt, 2005). Given similarities in macaque and human face processing (e.g., Dahl, Wallraven, Bülthoff, & Logothetis, 2009), this finding raises the possibility that dominance will also have a positive effect on the motivational salience of faces in humans.

Recent work on the perceptual dimensions that underlie social judgments of faces in humans has demonstrated that social judgments of faces can be reduced to orthogonal valence and dominance components (Oosterhof & Todorov, 2008). The valence component is highly correlated with traits such as perceived trustworthiness and attractiveness and appears to reflect perceptions of general prosociality (Oosterhof & Todorov, 2008). The dominance component is highly correlated with traits such as perceived dominance and aggressiveness and appears to reflect perceptions of capacity to inflect physical harm (Oosterhof & Todorov, 2008). Neurobiological evidence suggests that effects of attractiveness on neural markers of the motivational salience of faces may be better characterized as effects of the valence component than effects of attractiveness (see Bzdok et al., 2011). That male macaques find more dominant conspecifics' faces more rewarding (Deaner et al., 2005), suggests that the dominance component of social judgments of faces might also be associated with the motivational salience of faces in humans. This would be noteworthy because the motivational salience of faces is thought to drive the link between perceptual judgments and behavioral responses (Aharon et al., 2001; Hahn et al., 2016; Levy et al., 2008) and such results would suggest that the motivational salience of faces is not solely a consequence of their perceived valence.

The current study investigated whether the motivational salience of faces is positively and independently related to Oosterhof and Todorov's (2008) valence and dominance components. Motivational salience of faces was assessed using a standard key-press task that has been used in many previous studies of the motivational salience of faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2015; Wang et al., 2014). Responses to faces on this key-press task have been shown to predict neural markers of the reward value of faces (Aharon et al., 2001). Following Oosterhof and Todorov (2008), principal component analysis was used to reduce ratings of faces on multiple traits to valence and dominance components.

3.2 Methods

3.2.1 Face-rating task

Face stimuli were images of 50 white men and 50 white women. The face stimuli used in this study were the same face stimuli used in the study reported in Chapter 2 (see section 2.2.2).

Men (N=260) and women (N=260) who took part in the face-rating part of the study (mean age = 22.97 years, SD = 5.52 years) were randomly allocated to rate either male or female faces for one of the 13 traits investigated by Oosterhof and Todorov (2008) using 1(low) to 7(high) rating scales. All participants were between 16 and 40 years of age. These traits were aggressiveness, attractiveness, caringness, confidence, dominance, emotional stability, intelligence, meanness, responsibility, sociability, trustworthiness, unhappiness, weirdness. This process meant that 10 men and 10 women rated each combination of trait and face sex. Trial order within blocks was fully randomized. The study was run online at faceresearch.org, with participants recruited from social bookmarking websites, such as stumbleupon.com.

3.2.2 Key-press task

The same face images presented in the face rating part of the study were also used in the key-press task. The procedure of the key-press task used in this study is the same as the procedure used in the study reported in Chapter 2 (see section 2.2.3).

A different set of 300 heterosexual women (mean age = 21.77 years, SD = 4.15 years) and 300 heterosexual men (mean age = 24.79 years, SD = 5.63 years) completed a standard key-press task. All participants were between 16 and 40 years of age. One hundred and fifty men and 150 women were presented with images of the opposite-sex faces and the other 150 men and 150 women were presented with images of the same-sex faces. Participants were randomly allocated to only one version of the task (i.e., saw either male faces or female faces). Trial order within each block was fully randomized. This part of the study was also run online at faceresearch.org, again with participants recruited from social bookmarking websites, such as stumbleupon.com. Online and laboratory studies of the motivational salience of faces have typically shown similar patterns of results (Aharon et al., 2001, Hahn et al., 2013, 2016).

As described in section 2.2.3, in each version of the key-press task, participants controlled the viewing duration of each face image by repeatedly pressing designated keys on their keyboard after initiating each trial by pressing the space bar. Each key press increased or decreased the viewing duration by 100ms. The default viewing duration for each image (i.e., the length of time a face remained onscreen if no keys were pressed) was 4s.

3.2.3 Initial processing of data

Inter-rater agreement, as estimated by Cronbach's alpha, was high for all perceptual ratings of the male and female faces (see Table 3.1), with the exception of unhappiness, for which inter-rater agreement was low for both male and female faces (both Cronbach's alphas < .50). At this point, unhappiness was discarded from the study. All other perceptual ratings were standardized within face sex (i.e., scores for male faces and scores for female faces were separately converted to z-scores) to control for possible effects of differences in how male and female faces were rated. Descriptive statistics for each trait are shown in Table 3.1, together with results of independent samples t-tests comparing ratings of male and female faces.

Table 3.1. Descriptive statistics for all traits considered in our analyses and results (t and p statistics) for independent samples t-tests for differences between ratings of male and female faces for each trait.

	Male faces			Female faces				
Trait	**α**	***M***	***SD***	**α**	***M***	***SD***	***t***	***p***
Aggressiveness	0.90	3.31	0.86	0.80	3.65	0.68	2.18	.032
Attractiveness	0.91	2.77	0.72	0.88	3.03	0.60	1.98	.051
Caringness	0.81	3.58	0.70	0.84	3.37	0.67	-1.52	.132
Confidence	0.86	3.87	0.69	0.85	3.71	0.72	-1.11	.272
Dominance	0.90	3.44	0.81	0.81	3.45	0.66	0.13	.897
Emotional stability	0.84	3.77	0.64	0.71	3.62	0.53	-1.25	.216
Intelligence	0.78	3.75	0.62	0.70	3.77	0.47	0.23	.821
Meanness	0.75	4.05	0.60	0.82	3.84	0.68	-1.56	.122
Responsibility	0.84	3.56	0.66	0.69	3.88	0.50	2.73	.008
Sociability	0.91	3.55	0.76	0.84	3.75	0.70	1.37	.173
Trustworthiness	0.84	3.34	0.61	0.77	3.90	0.56	4.73	<.001
Weirdness	0.90	4.49	0.83	0.74	4.25	0.58	-1.63	.106

Note. All variables were subsequently standardized within face sex.

Following previous studies of the motivational salience of faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2015; Wang et al., 2014), key-press scores for each face were calculated by subtracting the number of key presses made to decrease viewing time from those made to increase viewing time. These scores were calculated separately for each participant and served as the dependent variable in our analyses. Faces with greater key press scores are those with greater motivational salience (Aharon et al., 2001). Because inter-participant agreement in key-press scores for both male and female faces were high (both Cronbach's alphas > .95), we calculated the average key-press score for each face. This was done separately for male participants (male faces: M=-6.04, SD=2.96; female faces: M=-4.81, SD=5.18) and female participants (male faces: M=-2.96, SD=5.25; female faces: M=-3.00, SD=4.03). As was the case for the perceptual ratings, these scores were standardized within face sex.

3.3 Results

Following previous studies that used principal component analysis to reveal the components underlying ratings of social stimuli (e.g., McAleer et al., 2014; Oosterhof & Todorov, 2008), we subjected all ratings to principal component analysis with no rotation. Two orthogonal components with eigenvalues greater than 1 were extracted. The first component explained approximately 50% of the variance in scores and was highly correlated with caringness, trustworthiness, and emotional stability. We labeled this the valence component. The second component explained approximately 24% of the variance in scores and was highly correlated with dominance and aggressiveness. We labeled this the dominance component. The component matrix is shown in Table 3.2. We used these two orthogonal components in our main analyses.

Table 3.2 Component matrix for principal component analysis of all traits.

Trait	Component 1 (valence)	Component 2 (dominance)
Aggressiveness	-0.56	0.76
Attractiveness	0.78	0.36
Caringness	0.88	-0.26
Confidence	0.57	0.67
Dominance	-0.03	0.91
Emotional stability	0.86	0.13
Intelligence	0.65	0.27
Meanness	-0.59	0.74
Responsibility	0.71	0.22
Sociability	0.84	0.13
Trustworthiness	0.86	-0.27
Weirdness	-0.73	-0.20

Note. We labeled the first component the *valence component* (explained ~50% of the variance in scores) and labeled the second component the *dominance component* (explained ~24% of the variance in scores).

Next, we analyzed key-press scores using ANCOVA with a custom model that included the within-items factor *participant sex* (male, female), the between-items factor *sex of face* (male, female), and scores on the *valence* and *dominance components* as covariates. The custom model included main effects of each factor and all possible two-way and three-way interactions, except ones including both the *valence* and *dominance components*.

This analysis revealed main effects of *valence* ($F(1,94)=105.00$, $p<.001$, partial $eta^2=.53$) and *dominance* ($F(1,94)=17.10$, $p<.001$, partial $eta^2=.15$), indicating faces that scored higher on the valence or dominance components generally had greater motivational salience (valence: $r=.70$, $N=100$, $p<.001$; dominance: $r=.28$, $N=100$, $p=.004$). Figures 3.1 and 3.2 show the scatter plots of valence and dominance components versus key-press scores respectively. Key-press score descriptive statistics for faces scoring ±1 SD from the mean on the valence and dominance components are given in Table 3.3. The correlation between valence and key-press scores was stronger than that between dominance and key-press scores ($z=3.82$, $p<.001$, Steiger, 1980). The interaction between *participant sex* and *valence* was not significance ($F(1,94)=3.25$, $p=.075$, partial $eta^2=.033$; female participants: $r=.72$, $N=100$, $p<.001$; male participants: $r=.63$, $N=100$, $p<.001$; see Figure 3.3). No other effects were significant or approached significant (all $F< 1.53$, all $p> .22$, see Tables 3.4 for full results of this model.).

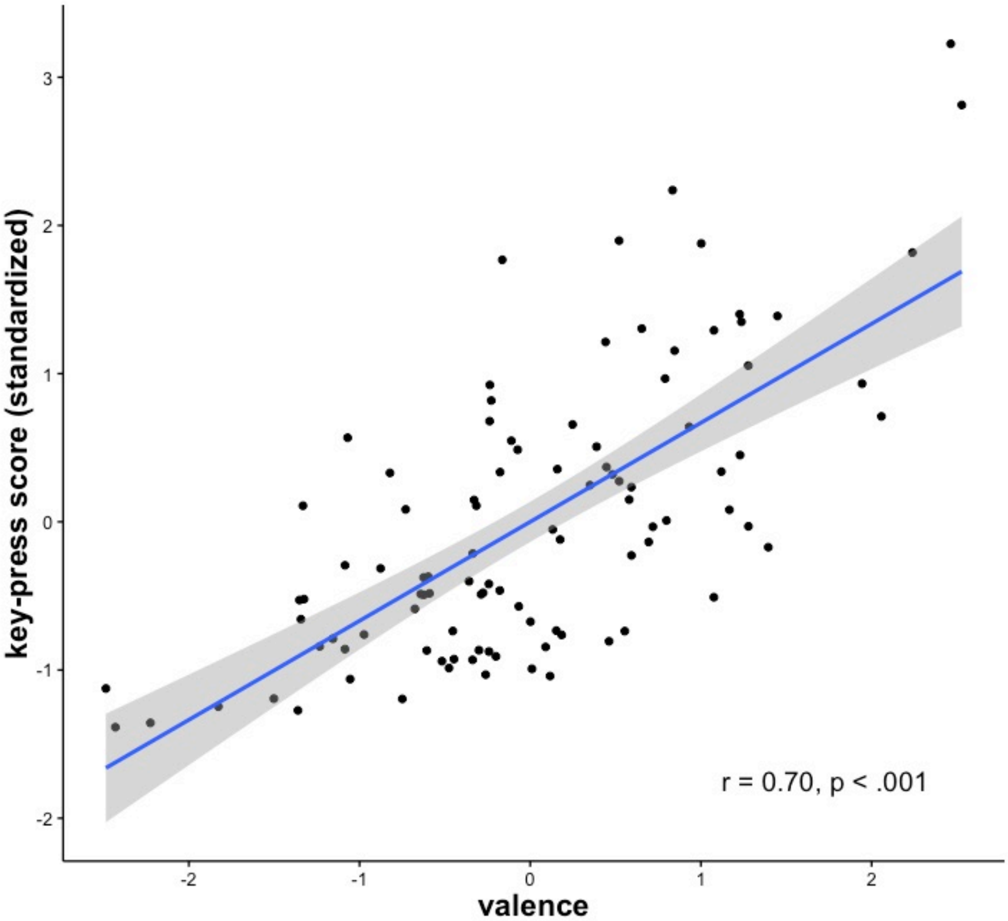

Figure 3.1 Scatter plot of valence component versus key-press scores and the regression line between valence component and key-press scores (the grey area is the 95% confidence interval).

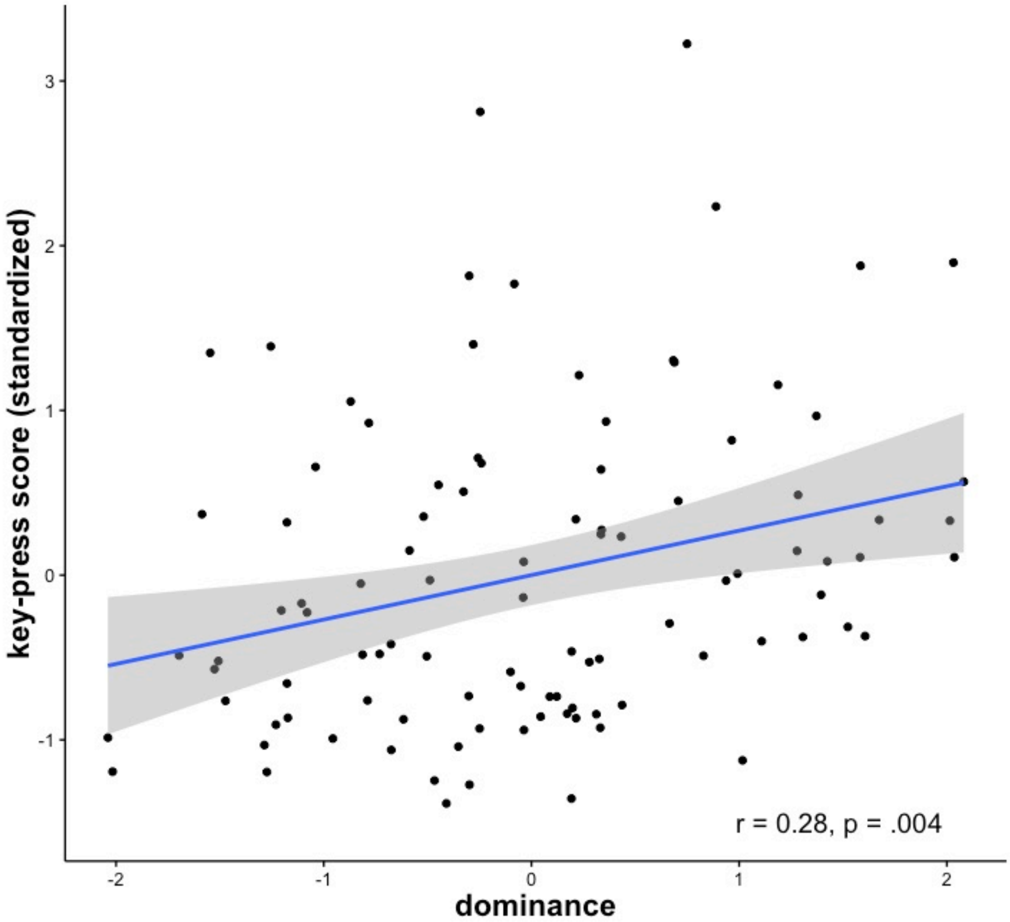

Figure 3.2 Scatter plot of dominance component versus key-press scores and the regression line between dominance component and key-press scores (the grey area is the 95% confidence interval).

Table 3.3 Descriptive statistics of key-press scores for faces scoring ±1 SD from the mean on the valence and dominance components.

Component	Band	Mean	SD
valence	1 SD above the mean	0.39	4.30
valence	1 SD below the mean	-7.46	2.54
dominance	1 SD above the mean	-2.90	3.53
dominance	1 SD below the mean	-5.41	3.60

Note. This table shows descriptive statistics for unstandardized key-press scores.

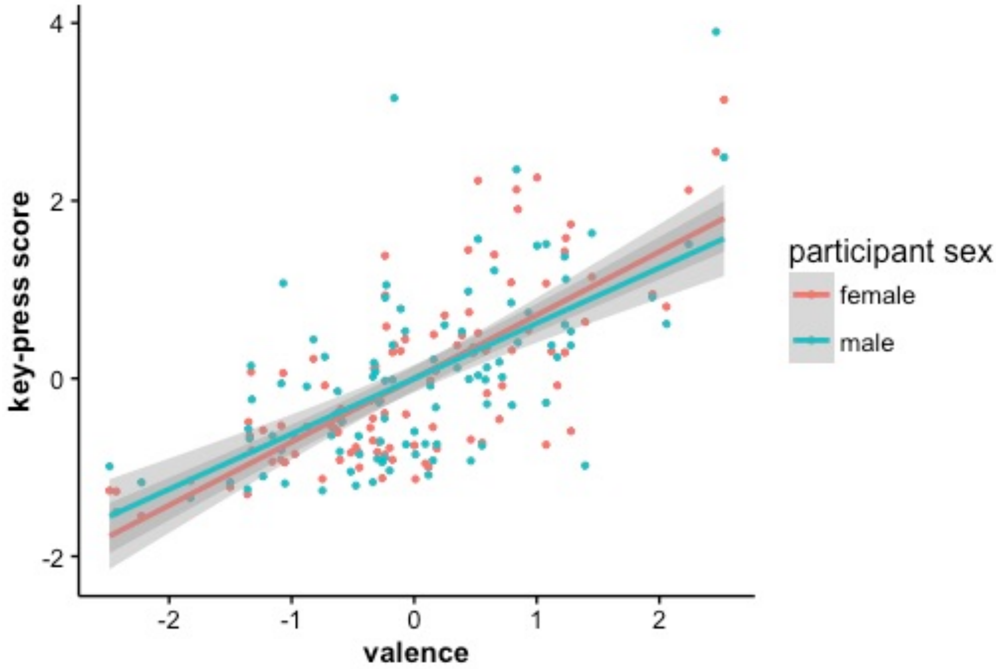

Figure 3.3 Correlation between valence component and key-press scores for female (red) and male faces (green)

Table 3.4 Full results of the analysis on key-press scores

Effect	**Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**	**Parti-al eta^2**
Intercept	0.00	1	0.00	0.00	1.00	.000
Valence	86.69	1	86.69	105.00	.00	.528
Dominance	14.11	1	14.11	17.10	.00	.154
Face sex	0.00	1	0.00	0.00	1.00	.000
Participant sex	0.00	1	0.00	0.00	1.00	.000
Face sex * valence	0.00	1	0.00	0.00	.994	.000
Face sex * dominance	0.10	1	0.10	0.12	.734	.000
Participant sex * face sex	0.00	1	0.00	0.00	1.00	.000
Participant sex * valence	0.50	1	0.50	3.25	.075	.033
Participant sex * dominance	0.24	1	0.24	1.53	.220	.016
Participant sex * face sex * valence	0.17	1	0.17	1.11	.296	.012
Participant sex * face sex * dominance	0.11	1	0.11	0.70	.404	.007
Error (between-item)	77.61	94	0.83			
Error (within-item)	14.57	94	0.16			

3.4 Discussion

Principal component analysis of the initial face ratings produced two orthogonal components. Replicating previous research that has used this method to reveal the components that underpin social judgments of faces Oosterhof and Todorov (2008), these components reflected the perceived valence and dominance of faces, respectively. Importantly, further analysis showed that both the valence and dominance components were positively and significantly correlated with the motivational salience of faces, as assessed from responses on a standard key-press task.

That faces scoring higher on the valence component had greater motivational salience is consistent with previous work reporting positive effects of attractiveness on the motivational salience of faces (Levy et al., 2008; Hahn et al., 2015; Wang et al., 2014). It is also consistent with neural evidence that overlapping brain networks drive the processing of facial attractiveness and facial trustworthiness (Bzdok et al., 2011).

Additionally, our analyses revealed systematic variation in the motivational salience of faces that was not due to valence, however. Faces that scored higher on the dominance component also had greater motivational salience. This effect of dominance on the motivational salience of faces complements results of studies of macaques, whereby male macaques were more willing to exchange juice rewards to view high-dominance, rather than low-dominance, conspecifics' faces (Deaner et al., 2005). Positive correlations between facial dominance and cues of physical strength and aggression in humans have been widely reported (reviewed in Puts, 2010). Thus, greater motivational salience of more dominant faces may function, in part, to support the monitoring of individuals with high threat potential during social interactions. Note that, while male macaques were more willing to exchange juice rewards to view high-dominance faces (Deaner et al., 2005), our participants showed smaller negative key-press scores for high-dominance faces, rather than larger positive key-press scores. Although it is tempting to interpret this pattern of results as indicating that high-dominance faces are less aversive, rather than more rewarding, to humans, this distinction between negative and positive key-press scores could simply reflect the length of the default viewing time (4s). Using a shorter default viewing time could reveal positive key-press scores for high-dominance faces.

Previous research has suggested that facial cues of dominance in conspecifics have similar effects on macaques' and human's responses to gaze-direction cues (Jones et al., 2010; Shepherd et al., 2006). Our results linking dominance to the motivational salience of faces then present new evidence for similarities in human and macaque responses to facial dominance by extending results for motivational salience of facial cues of conspecifics' dominance in macaques to human participants. Our face stimuli all had neutral expressions and direct gaze. Since emotional expressions and gaze direction can modulate responses to physical characteristics in faces (Gill, Garrod, Jack, & Schyns, 2014; Jones, DeBruine, Little, Conway, & Feinberg, 2006; Van den Stock, & de Gelder, 2014), further work is needed to establish how these cues might modulate the motivational salience of valence and dominance.

While the work reported in Chapter 2 investigated within-woman differences in the motivational salience of facial attractiveness, Chapter 3 demonstrated that facial dominance also contributes to the general motivational salience of faces. While these chapters did not examine between-woman differences in responses to facial attractiveness, Chapter 4 examined whether women's responses to facial attractiveness differ as a function of their romantic partnership status.

Chapter 4

Do partnered women discriminate men's faces less along the attractiveness dimension?

This chapter is based on work published in Personality and Individual Differences.

Wang, H., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2016). Do partnered women discriminate men's faces less along the attractiveness dimension? *Personality and Individual Differences*, 98, 153-156.

Abstract

Romantic relationships can have positive effects on health and reproductive fitness. Given that attractive potential alternative mates can pose a threat to romantic relationships, some researchers have proposed that partnered individuals discriminate opposite-sex individuals less along the physical attractiveness dimension than do unpartnered individuals. This effect is proposed to devalue attractive (i.e., high quality) alternative mates and help maintain romantic relationships. Here we investigated this issue by comparing the effects of men's attractiveness on partnered and unpartnered women's performance on two response measures for which attractiveness is known to be important: memory for face photographs (Study 1) and the reward value of faces (Study 2). Consistent with previous research, women's memory was poorer for face photographs of more attractive men (Study 1) and more attractive men's faces were more rewarding (Study 2). However, in neither study were these effects of attractiveness modulated by women's partnership status or partnered women's reported commitment to or happiness with their romantic relationship. These results do not support the proposal that partnered women discriminate potential alternative mates along the physical attractiveness dimension less than do unpartnered women.

4.1 Introduction

Romantic relationships have positive effects on reproductive fitness by increasing resources available for investment in offspring (Buss & Schmitt, 1993). Romantic relationships also have positive effects on both physical and psychological health (House et al., 1988). Given the importance of physical attractiveness for human mate choice (e.g., Thornhill & Gangestad, 1999), several researchers have proposed that partnered individuals might discriminate opposite-sex individuals along the physical attractiveness dimension less than do unpartnered individuals (Karremans et al., 2011; Ritter et al., 2010). These differences are thought to function to devalue attractive (i.e., high quality, Thornhill & Gangestad, 1999) alternative mates (Karremans et al., 2011; Ritter et al., 2010). Devaluing attractive alternative mates may help to maintain romantic relationships by reducing the likelihood of the pursuit of alternative mates.

Recent evidence for the proposal described above has come from research that used a reverse-correlation technique (Mangini & Biederman, 2004) to visualize heterosexual women's internal representations of previously seen attractive and unattractive men's faces (Karremans et al., 2011). Karremans et al. (2011) found that partnered women's internal representations of *attractive* men's faces were *less* attractive than those of unpartnered women, By contrast, partnered women's representations of *unattractive* men's faces were *more* attractive than those of unpartnered women. These results were interpreted as evidence that partnered women discriminate men's faces along the physical attractiveness dimension less. This interpretation is consistent with findings from other studies where, when instructed to disregard their own current partnership status, partnered participants are less likely to identify physically attractive individuals as potential romantic partners than are unpartnered participants (Ritter et al., 2010). They are also consistent with research where partnered individuals rated photographs of highly attractive people to be less attractive than did unpartnered individuals (Simpson et al., 1990).

The aim of the current study was to test for further evidence that partnered women discriminate men's faces along the physical attractiveness dimension less than do unpartnered women. We did this by comparing the effects of men's facial attractiveness on partnered and unpartnered women's performance on two measures for which attractiveness is known to be important. In Study 1, we assessed partnered and unpartnered women’s memory for photographs of men’s faces using an “old-new” memory task (Macmillan & Creelman, 2005), in which women watched a slideshow of images of men’s faces that had previously been rated for attractiveness by a different group of participants. The women were then shown both these face images and foil images (i.e., were shown these “old” face images interspersed among previously unseen “new” male face images), and were asked to indicate whether or not they had seen each face photograph before. Previous research suggests that more attractive faces are less memorable (e.g., Wiese et al., 2014), but has not investigated the possible effects of women’s partnership status. If partnered women discriminate men’s faces along the physical attractiveness dimension less than do unpartnered women (Karremans et al., 2011), the predicted negative effect of attractiveness on the memorability of photographs of men’s faces should be weaker in partnered than unpartnered women.

In Study 2, we used a standard key-press task (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015; Wang et al., 2014) to assess the reward value of images of men’s faces in partnered and unpartnered women. In this task, participants can control the length of time for which they view faces by repeatedly pressing keys to either increase or decrease the viewing time (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015; Wang et al., 2014). Responses on this type of key-press task are a better predictor of neural measures of the reward value and motivational salience of face images than attractiveness ratings (Aharon et al., 2001). As in Study 1, our male face stimuli had previously been rated for attractiveness by a different group of participants. The same face stimuli were used in both studies. Previous research has found that more attractive male faces have greater reward value to women (Levy et al., 2008; Hahn et al., 2014, 2015; Wang et al., 2014). However, this work has not considered the possible effects of women’s partnership status. If partnered women discriminate men’s faces along the physical attractiveness dimension less than do unpartnered women, the predicted positive effect of attractiveness on the reward value of men’s faces should be weaker in partnered than unpartnered women.

4.2 Study 1

The aim of Study 1 was to test whether the effect of facial attractiveness on women’s memory for photographs of men’s faces was different for partnered and unpartnered women. Weaker effects of facial attractiveness on partnered women’s memory for photographs of men's faces would support the proposal that partnered women differentiate men's faces along the attractiveness dimension less.

4.2.1 Methods

Attractiveness ratings

Face stimuli were images of 50 young adult white men. The face stimuli used in this study were the same face stimuli used in studies reported in Chapters 2 and 3 (see section 2.2.2).

The 50 male face images were rated for attractiveness by 100 heterosexual women and 100 heterosexual men (mean age=24.67 years, SD=5.87 years; range: 18 to 40.7 years) using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. Trial order was fully randomized. This part of the study was run online, with participants recruited from links on social bookmarking websites (e.g., stumbleupon.com). Participants did not receive any payment. Inter-rater agreement was high for these ratings (Cronbach's α=.99) and mean ratings derived from female and male raters' scores were highly correlated (r=.97, N=50, p<.001). Thus, we combined ratings from female and male raters to produce a single attractiveness score for each face. These average scores were used in our main analyses.

Memory task

The same face images presented in the face rating part of the study were also used in the memory task, which was completed by 350 heterosexual women (mean age=22.65 years, *SD*=5.43 years; range: 16 to 39.7 years) who had not taken part in the rating part of the study. These participants reported whether they were currently in a romantic relationship (N=165) or currently not in a romantic relationship (N=185) by answering yes or no to the question "Do you have a partner? (e.g. a boyfriend, husband, etc.)". Participants who reported being in a romantic relationship also reported how happy they were in their relationship with their partner (M=5.72, SD=1.37) and how committed they were to their relationship with their partner (M=5.87, SD=1.34) using 1 (much less happy/committed than average) to 7 (much more happy/committed than average) rating scales.

In an initial exposure phase, participants were shown half of the male faces. In this exposure phase, images were presented in a fully randomized order and each image shown once for 2000ms (i.e., the exposure phase lasted 50 seconds in total). In a test phase immediately after the exposure phase, participants were shown all of the male faces, again in a fully randomized order, and were asked to indicate whether or not they had seen each face during the exposure phase. Which individual faces were shown during the exposure phase was counterbalanced across participants. Participants were told prior to the exposure phase that it would be followed by a memory test. This part of the study was also run online. Participants were again recruited from links on social bookmarking websites and did not receive any payment.

For each face, we used the proportion of women who correctly identified it as having been seen previously to calculate the hit rate for performance on the memory task. This was calculated separately for partnered women (M=.78, SD=.09) and unpartnered women (M=.78, SD=.09). The proportion of women who incorrectly identified a face as having been seen previously was used to calculate the corresponding false alarm rate for each face. Again, this was calculated separately for partnered women (M=.21, SD=.12) and unpartnered women (M=.20, SD=.12). Hit rates and false alarm rates were used to calculate d-prime for each face separately for partnered women (M=1.73, SD=0.69) and unpartnered women (M=1.74, SD=0.64). We used d-prime in our analyses because it is an unbiased measure of memory performance that considers both the hit and false-alarm rates (i.e., it takes into account response bias, Macmillan & Creelman, 2005).

4.2.2 Results

First, d-prime was analyzed using ANCOVA, with *men's facial attractiveness* as the covariate and *women's partnership status* (partnered, unpartnered) as a within-items factor. There was a significant main effect of *men's facial attractiveness* ($F(1,48)=12.66$, $p=.001$, partial $eta^2=.21$). Neither the main effect of *women's partnership status* nor the interaction between *women's partnership status* and *men's facial attractiveness* were significant (both $F(1,48)<0.52$, both $p>.47$, both partial $eta^2<.01$, see Figure 4.1). The main effect of *men's facial attractiveness* indicated that memory was poorer for more attractive male faces (overall: r=–.47, N=50, p=.001; partnered women: r=-.45, N=50, p=.001; unpartnered women: r=-.43, N=50, p=.002).

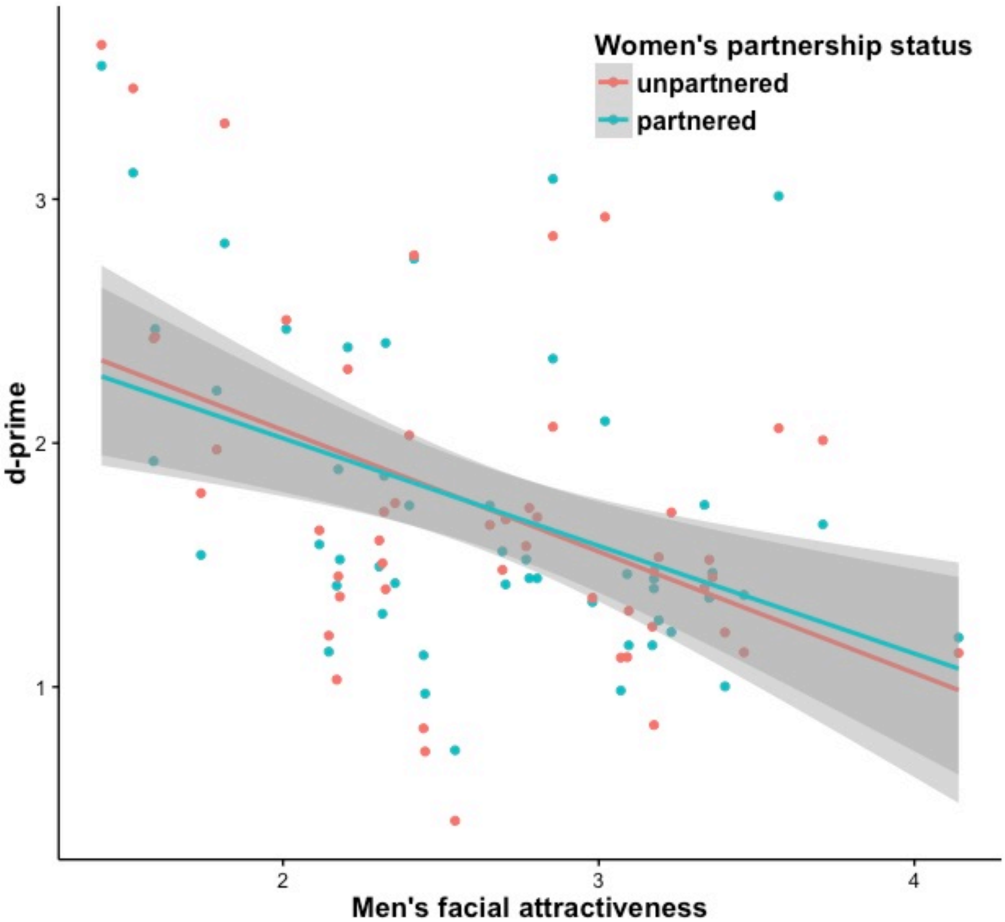

Figure 4.1 Scatter plot of men's facial attractiveness versus d-prime and the regression line between men's facial attractiveness and d-prime (the grey area is the 95% confidence interval) separately for partnered (green) and unpartnered women (red).

Next, we tested whether the effect of attractiveness on memory for faces differed between partnered women who reported being committed to and happy in their relationship and those who reported being less committed to and less happy in their relationship. Because partnered women's relationship happiness and commitment ratings were highly and positively correlated ($r=.55$, $N=165$, $p<.001$), we converted the relationship happiness and commitment ratings to z-scores and averaged them. We then separately calculated d-prime for those partnered women who scored above the median on the combined relationship commitment/happiness score and those partnered women who scored below the median on the combined relationship commitment/happiness score. Analyzing these scores using ANCOVA, with *men's facial attractiveness* as the covariate and *women's relationship type* (high commitment and happiness, low commitment and happiness) as a within-items factor showed a significant main effect of *men's facial attractiveness* (F(1,48)=14.61, $p<.001$, partial $eta^2=.23$) and *women's relationship type* (F(1,48)=5.13, $p=.03$, partial $eta^2=.10$). The interaction between *women's relationship type* and *men's facial attractiveness* was not significant (F(1,48)=2.24, $p=.14$, partial $eta^2=.04$, see Figure 4.2). The main effect of *men's facial attractiveness* indicated that memory was poorer for more attractive male faces (overall: r=–.45, N=50, p=.001; high commitment and happiness group: r=-.43, N=50, p=.002; low commitment and happiness group: r=-.49, N=50, p<.001). And the main effect of *women's relationship type* indicated that memory for male faces were poorer among women who scored high in commitment and happiness than those scored low in commitment and happiness. That the interaction between *men's facial attractiveness* and *women's relationship type* was not significant suggests that the effect of men's attractiveness on partnered women's memory for men's faces is not affected by the women's reported commitment to and happiness with their current romantic relationship.

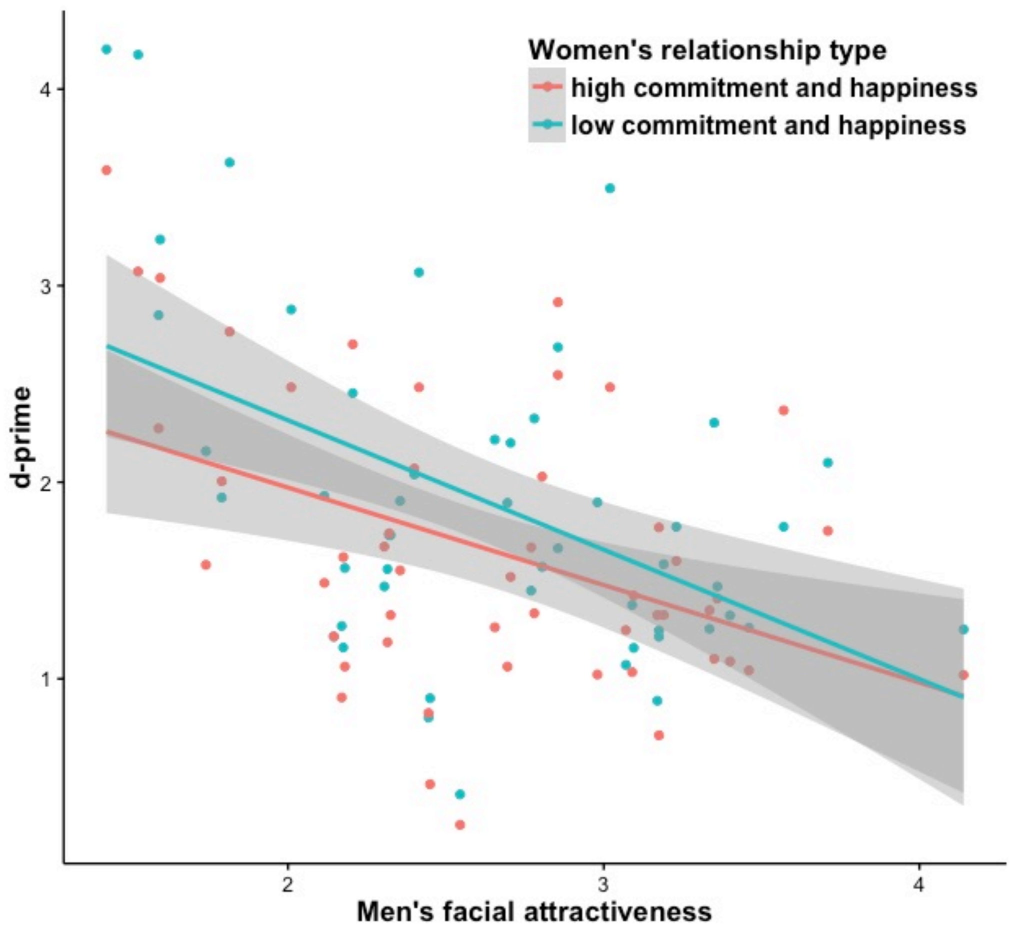

Figure 4.2 Scatter plot of men's facial attractiveness versus d-prime and the regression line between men's facial attractiveness and d-prime (the grey area is the 95%

confidence interval) separately for women scored low in commitment and happiness (green) and those scored high in commitment and happiness (red).

4.3 Study 2

The aim of Study 2 was to test whether the effect of facial attractiveness on the reward value of men's faces to women was different for partnered and unpartnered women. Weaker effects of facial attractiveness on the reward value of men's faces in partnered women would support the proposal that partnered women differentiate men's faces along the attractiveness dimension less.

4.3.1 Methods

The same face stimuli used in this Study 1 were also used in Study 2. The procedure of the key-press task used in this study was the same as the procedure used in studies reported in Chapters 2 and 3 (see section 2.2.3).

One thousand heterosexual women (mean age=21.97 years, *SD*=4.55 years; range: 16 to 40 years) took part in the study. These participants reported whether they were currently in a romantic relationship (N=500) or currently not in a romantic relationship (N=500) by answering yes or no to the question "Do you have a partner? (e.g. a boyfriend, husband, etc.)". Using the same 7-point scales we used in Study 1, participants who reported being in a romantic relationship also reported how happy they were in their relationship with their partner (M=5.59, SD=1.44) and how committed they were to their relationship with their partner (M=5.84, SD=1.40). Three partnered participants opted not to report this information. All participants completed a standard key-press task, similar to those used to assess the reward value of faces in previous studies (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2014, 2015; Wang, 2004). This part of the study was run online. Participants were recruited from links on social bookmarking websites and did not receive any payment. Previous research has reported similar effects of attractiveness on the reward value of men's faces in studies conducted in the laboratory (Levy et al., 2008; Wang et al., 2014) and those conducted online (Hahn et al., 2014, 2015).

As described in section 2.2.3, the 50 male faces were presented in a fully randomized order. Participants controlled the viewing duration of each face image by repeatedly pressing designated keys on their keyboard after initiating each trial by pressing the space bar. Each key press increased or decreased the viewing duration by 100ms. The default viewing duration for each image (i.e., the length of time a face remained onscreen if no keys were pressed) was 4 seconds.

As described in section 2.2.3, key-press scores for each face were calculated by subtracting the number of key presses made to decrease viewing time from those made to increase viewing time. Inter-rater agreement was high for the key-press scores for both partnered (Cronbach's α=.89) and unpartnered women (Cronbach's α=.87). These scores were averaged for each face separately for partnered women ($M=-3.87$, $SD=4.84$) and unpartnered women ($M=-3.18$, $SD=5.57$) and served as the dependent variable in our analysis. Faces with greater key press scores are those with greater reward value (Aharon et al., 2001). The mean attractiveness ratings of men's faces from Study 1 were also used in our analysis of key-press scores in Study 2.

4.3.2 Results

Similar to the analysis used in Study 1, key-press scores were analyzed using ANCOVA, with *men's facial attractiveness* as the covariate and *women's partnership status* (partnered, unpartnered) as a within-items factor. There was a significant main effect of *men's facial attractiveness* ($F(1,48)=78.46$, $p<.001$, partial eta^2=.62). Neither the main effect of *women's partnership status* nor the interaction between *women's partnership status* and *men's facial attractiveness* were significant (both $F(1,48)<1.31$, both $p>.25$, both partial eta^2<.03, see Figure 4.3). The main effect of *men's facial attractiveness* indicated that the reward value of men's faces was more pronounced for more attractive male faces (overall: $r=.79$, $N=50$, $p<.001$; partnered women: $r=.82$, $N=50$, $p<.001$; unpartnered women: $r=.75$, $N=50$, $p<.001$).

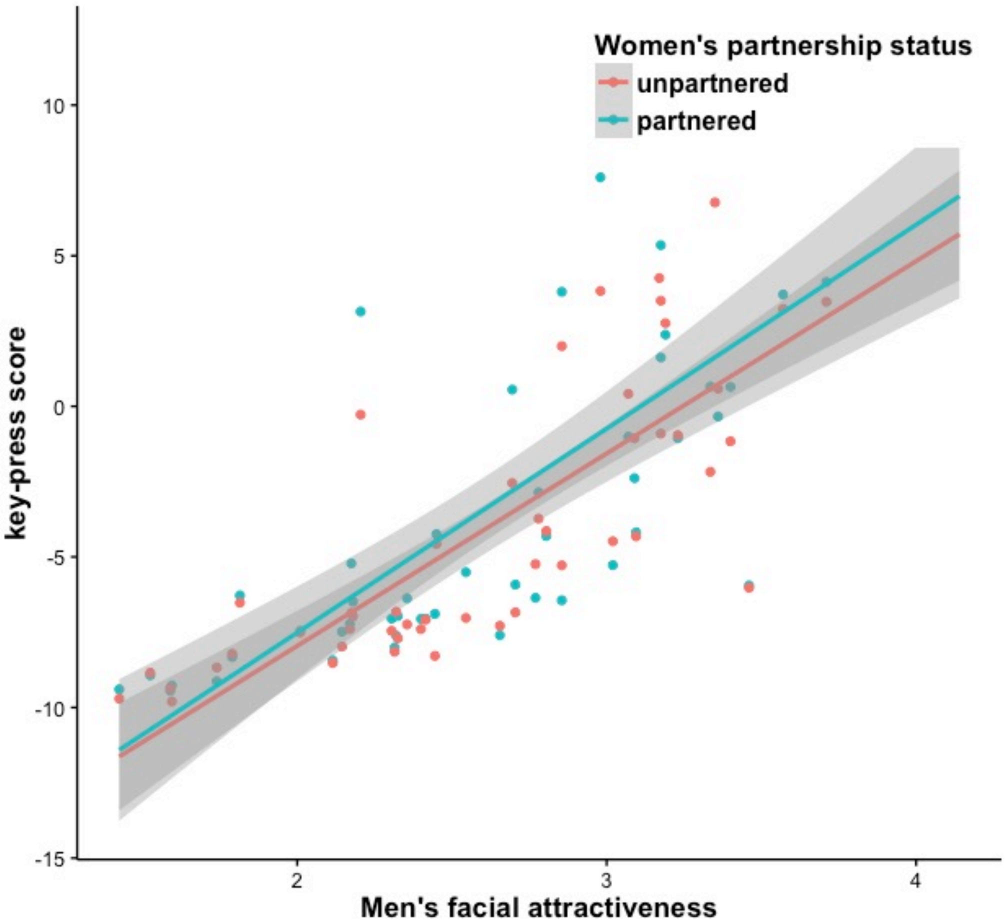

Figure 4.3 Scatter plot of men's facial attractiveness versus key-press scores and the regression line between men's facial attractiveness and key-press scores (the grey area is the 95% confidence interval) separately for partnered (green) and unpartnered women (red).

Next, we tested whether the effect of attractiveness on key-press scores differed between partnered women who reported being committed to and happy in their relationship and those who reported being less committed to and less happy in their relationship. As in Study 1, women's relationship happiness and commitment ratings were highly and positively correlated ($r=.63$, $N=497$, $p<.001$), so we converted these ratings to z-scores and averaged them. We then separately calculated mean key-press scores for those partnered women who scored above the median on the combined relationship commitment/happiness score and those partnered women who scored below the median on the combined relationship commitment/happiness score. Analyzing these scores using ANCOVA, with *men's facial attractiveness* as the covariate and *women's relationship type* (high commitment and happiness, low commitment and happiness) as a within-items factor showed a significant main effect of *men's facial attractiveness* ($F(1,48)=101.66$, $p<.001$, partial $eta^2=.68$), but not a main effect of *women's relationship type* ($F(1,48)=1.22$, $p=.28$, partial $eta^2=.03$). The interaction between *women's relationship type* and *men's facial attractiveness* was also not significant ($F(1,48)=3.35$, $p=.07$, partial $eta^2=.07$, see Figure 4.4). The main effect of *men's facial attractiveness* indicated that the reward value of men's faces was more pronounced for more attractive male faces (overall: $r=.82$, $N=50$, $p<.001$; high commitment and happiness group: $r=.79$, $N=50$, $p<.001$; low commitment and happiness group: $r=.84$, $N=50$, $p<.001$). These results suggest that the effect of men's attractiveness on the reward value of men's faces is not significantly affected by the women's reported commitment to and happiness with their current romantic relationship.

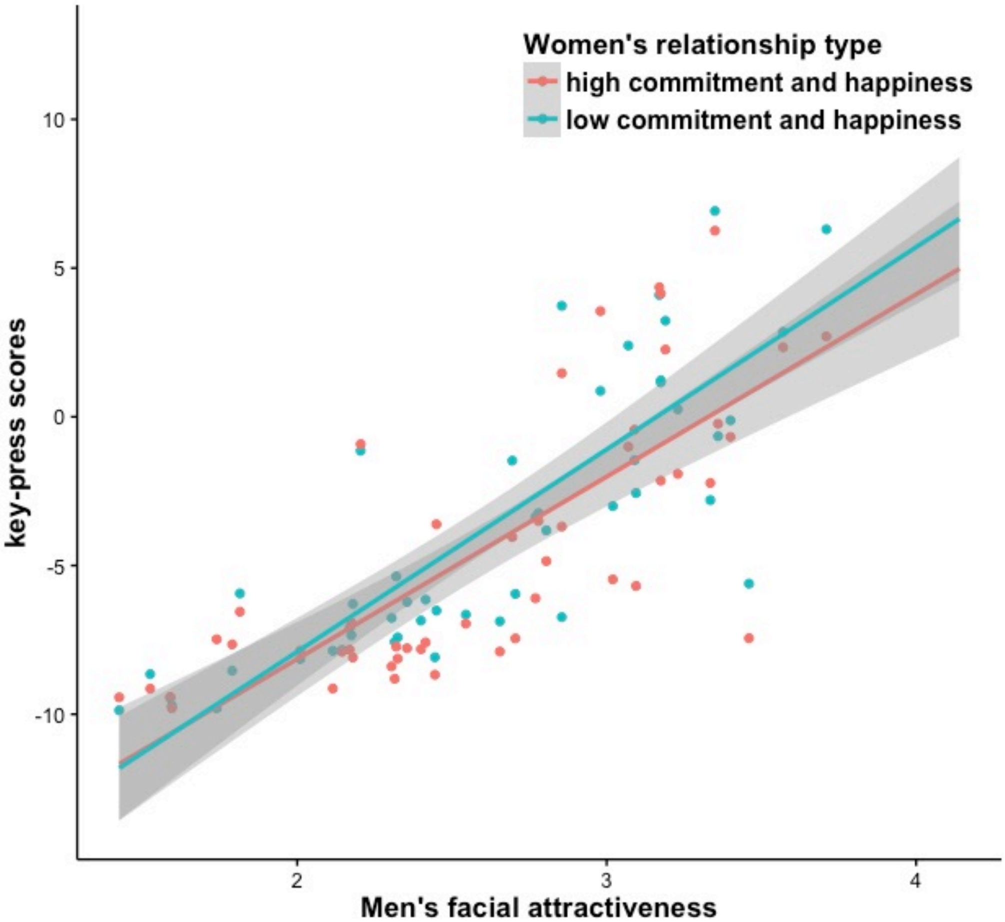

Figure 4.4 Scatter plot of men's facial attractiveness versus key-press scores and the regression line between men's facial attractiveness and key-press scores (the grey area is the 95% confidence interval) separately for women scored low in commitment and happiness (green) and those scored high in commitment and happiness (red).

4.4 Discussion

In Study 1, there was a negative correlation between d-prime scores and facial attractiveness, indicating that women's memory was generally poorer for photographs of more attractive men's faces. This pattern of results is consistent with other recent work that reported poorer memory for more attractive faces (e.g., Wiese et al., 2014). Although distinctiveness ratings of faces are negatively correlated with attractiveness (Rhodes, 2006) and positively correlated with face memorability (e.g., Valentine, 1991), recent work has shown that the effects of distinctiveness alone do not explain poorer memory for more attractive faces (Wiese et al., 2014).

In Study 2, attractiveness had a positive effect on key-press scores for men's faces, indicating that more attractive men's faces were more rewarding to women. This pattern of results is consistent with previous research that also reported positive effects of attractiveness on this measure of the reward value of men's faces (Levy et al., 2008; Hahn et al., 2014, 2015; Wang et al., 2014).

While both studies show that women generally discriminate men's faces along the attractiveness dimension, we found no evidence that the relationships between attractiveness and memory for men's faces or attractiveness and the reward value of men's faces were significantly different for partnered and unpartnered women or for partnered women who scored above or below the median on a combined relationship happiness and commitment score. Thus, our data do not support the proposal that partnered women discriminate men's faces along the attractiveness dimension less than do unpartnered women. Consequently, while previous research has shown that partnered and unpartnered women's internal representations of previously seen attractive and unattractive men's faces appear to differ (Karremans et al., 2011), these representational differences do not appear to be sufficient to cause comparable differences in the effects of attractiveness on face memory or the reward value of faces. Nonetheless, we note here that the interaction between partnered women's commitment to / happiness with their relationship and male attractiveness approached significance in Study 2 ($p=.07$). This suggests that partnered women's commitment to / happiness with their relationship may have a weak effect on the extent to which they find attractive male faces rewarding. However, the attractiveness effect for partnered women in the high-happiness group ($r = .79$), while lower than the effect for women in the low-happiness group (r = .84), was still stronger than the effect for women in the unpartnered group (r = .75).

Previous research has reported that participants in a committed relationship were less likely to attend to attractive opposite-sex faces than were participants who were not in a committed relationship, but only if their mating motivation had been primed (Maner, Gailliot, & Miller, 2009). Other work reported that participants in a committed relationship rated the attractiveness of attractive opposite-sex individuals lower than participants who were not in a committed relationship did, but only when they were instructed that the target individual was romantically unattached (Lydon, Fitzsimons, & Naidoo, 2003). These findings suggest that effects of women's partnership status on their sensitivity to men's attractiveness could be contingent on factors such as the women's own mating motivation and/or beliefs about the target's availability. These results, together with our own null results for effects of women's partnership status and partnered women's relationship commitment and happiness, suggest that women's own relationship status contributes little to individual differences in the extent to which they discriminate among men based on their attractiveness. That effects of women's partnership status on their sensitivity to men's attractiveness can be contingent on factors such as the women's own mating motivation and/or beliefs about the target's availability may explain why some studies have observed clear differences between partnered and unpartnered women in the extent to which they discriminate men on the attractiveness dimension (Karremans et al., 2011) while others have not. Other factors that have been found to influence women's responses to attractive faces, such as changes in their hormone levels (Wang et al., 2014), could also have obscured between-group differences in sensitivity to facial attractiveness. Another potential reason for discrepancies in results is that, while some studies have included stimuli representing a diverse range of attractiveness (e.g., the current study), others have compared responses to stimuli of high and average attractiveness only (Maner et al., 2009).

Karremans et al. (2011) previously reported that partnered women's internal representations of *attractive* men's faces were *less* attractive than those of unpartnered women, but that their representations of *unattractive* men's faces were *more* attractive than those of unpartnered women. They suggested (1) that these results indicated that partnered women discriminated men's faces along the physical attractiveness dimension less than unpartnered women and (2) that this may help maintain partnered women's romantic relationships by devaluing attractive alternative mates. However, having more attractive representations of *un*attractive men's faces would potentially cause women to perceive unattractive (i.e., low quality, Thornhill & Gangestad, 1999) alternative mates to be more attractive than they actually are, which could have negative consequences for their reproductive fitness if this increases the chances of women choosing unattractive mates for extra-pair or replacement mates. This possibility raises questions about the extent to which the type of biased representations of male faces reported by Karremans et al. (2011) for partnered women would necessarily benefit their reproductive fitness. Indeed, other researchers have suggested that women's reproductive fitness may actually benefit from extra-pair mating with high quality mates (e.g., Gangestad & Simpson, 2000). Doing so would require that partnered women retain the ability to discriminate potential mates along the attractiveness dimension. Consistent with the possibility that discriminating among men on the attractiveness (i.e., quality) dimension may be beneficial to *both* partnered and unpartnered women, our studies showed no differences between partnered and unpartnered women's sensitivity to male facial attractiveness on two measures for which attractiveness is known to be important (memory for faces and the reward value of faces).

A key result from research reported in this chapter was that more attractive faces were harder to remember. The work described in Chapter 5 will build on this result by investigating the different characteristics that contribute to the memorability of face photographs.

Chapter 5

The components underlying traits that predict the memorability of face photographs

Abstract

Research into the characteristics that predict the memorability of face photographs traditionally emphasizes relationships with typicality, familiarity, and memorability ratings. However, more recent work suggests that ratings of social traits, such as attractiveness, intelligence, and responsibility, predict the memorability of face photographs independently of typicality, familiarity, and memorability ratings. What components underlie these traits is unclear, however, as is how these components relate to the actual memorability of face photographs. To investigate these issues, we (1) assessed the memorability of face photographs using an "old-new" memory test, (2) had the faces rated for a diverse range of social traits often considered in social perception research (e.g., trustworthiness, attractiveness, dominance), and (3) had the faces rated for traits traditionally emphasized in traditional work on the memorability of face photographs (e.g., typicality, familiarity, memorability). Principal component analysis of all these face ratings produced three orthogonal components that were highly correlated with trustworthiness, dominance, and memorability ratings, respectively. Importantly, each of these orthogonal components also predicted the actual memorability of face photographs. Collectively, these results suggest that the rated memorability of faces can be isolated from social judgments of faces and clarify the components that underlie traits predicting the memorability of face photographs.

5.1 Introduction

Establishing the characteristics of a face photograph that contribute to its memorability has potentially important applications, such as informing the design of techniques for learning highly and less memorable faces (Bainbridge et al., 2013). Early studies of this issue typically emphasized negative relationships between typicality and familiarity ratings of images and their memorability and a positive relationship between memorability ratings of images and their actual memorability (e.g., Vokey & Read, 1992). These dimensions have dominated research on the memorability of face photographs (Bainbridge et al., 2013).

Evaluations on social traits of faces (e.g., judgments of their attractiveness, trustworthiness, dominance, and aggressiveness) are made very rapidly (<100ms, Willis & Todorov, 2006) and guide social behavior. For example, people are more likely to cooperate with individuals whose facial appearance is rated as more trustworthy (Van't Wout & Sanfey, 2008). Social traits of faces (e.g., judgments of their attractiveness, trustworthiness, dominance, and aggressiveness) can be reduced to two orthogonal components (Oosterhof & Todorov, 2008). The first ("valence") is highly correlated with trustworthiness and attractiveness ratings. The second ("dominance") is highly correlated with dominance and aggressiveness ratings. These social traits predict the memorability of face photographs independently of traits more commonly emphasized in research on this topic (Oosterhof & Todorov, 2008). For example, hit rates are lower for faces rated high on attractiveness and intelligence and false alarm rates are greater for faces rated high on attractiveness and responsibility, even when controlling for the effects of typicality, familiarity, and memorability (Bainbridge et al., 2013). Collectively, these results suggest that ratings of traits that are traditionally emphasized in work on social judgments of faces and those traditionally emphasized in work on memorability can independently predict the memorability of face photographs (Bainbridge et al., 2013). Indeed, images of attractive faces are harder to remember than those of relatively unattractive faces, even when the faces are matched for distinctiveness (Wiese et al., 2014).

These studies demonstrate that many different traits of face images contribute to the memorability of face photographs. However, the components that underlie ratings of these traits, as well as how these components relate to the memorability of face photographs, are unclear. One possibility is that traits traditionally emphasized in studies of the memorability of face photographs (i.e., typicality, familiarity, and memorability ratings) are entirely subsumed under Oosterhof and Todorov's (2008) valence and dominance components. Consistent with this possibility, Oosterhof and Todorov (2008) reported that the rated 'weirdness' of face photographs was strongly and negatively correlated with the valence component. Indeed, Vokey and Read (1995) reported that the effects of typicality and attractiveness on memory for faces were completely explained by the effects of perceived familiarity and memorability components. Another possibility is that some of the traits emphasized in traditional studies of the memorability of face photographs are uncorrelated with Oosterhof and Todorov's (2008) valence and dominance components. Consistent with this possibility, some individual social judgments predict the memorability of face photographs independently of traits like typicality (Bainbridge et al., 2013).

In light of the above, I assessed the memorability of face photographs using a memory task in which participants watched a slideshow of face images, were then shown both these face images and foil images and asked to indicate whether or not they had seen each face photograph before. Different participants rated the faces for the 19 social traits considered in Bainbridge et al.'s (2013) study. We used principal component analysis to reveal the components underlying ratings of these traits. We then investigated the relationships between these components and the memorability of the face photographs.

5.2 Methods

5.2.1 Participants and procedure

Face stimuli were images of 50 white men and 50 white women. The face stimuli used in this study were the same face stimuli used in studies reported in Chapters 2, 3 and 4 (see section 2.2.2).

Men (N=380) and women (N=380) participating in the face rating part of the study (mean age=23.4 years, SD=5.66 years) were randomly allocated to rate either male or female faces for one of the 19 traits investigated by Bainbridge et al. (2013) using 1 (low) to 7 (high) rating scales[1]. These traits were the 13 traits (aggressiveness, attractiveness, caringness, confidence, dominance, emotional stability, intelligence, meanness, responsibility, sociability, trustworthiness, unhappiness, weirdness) considered in Oosterhof and Todorov (2008), the three traits (typicality, memorability, familiarity) considered in Vokey and Read (1992), and three additional traits (commonness, emotionality, friendliness) considered only in Bainbridge et al. (2013).

[1] The 13 traits (aggressiveness, attractiveness, caringness, confidence, dominance, emotional stability, intelligence, meanness, responsibility, sociability, trustworthiness, unhappiness, weirdness) were rated by the same participants in Chapter 3.

This meant that 10 men and 10 women rated each combination of trait and face sex. That different participants rated each trait is consistent with other studies that have investigated the components underlying social judgments (McAleer et al., 2014; Oosterhof & Todorov, 2008) and avoids carry-over effects that occur when the same participants rate faces for multiple traits (Rhodes, 2006). Following other studies that have investigated the components underlying social judgments, traits were not defined for participants (McAleer et al., 2014; Oosterhof & Todorov, 2008) and male and female stimuli were rated in separate blocks of trials (McAleer et al., 2014). The study was run online at faceresearch.org, with participants recruited from social bookmarking websites, such as stumbleupon.com. Trial order within blocks was fully randomized.

The images from the face rating part of the study were also used in the memory task, which was completed by a different 160 men and 160 women (mean age=23.4 years, SD=5.52 years). The procedure of the memory task is the same as the procedure used in the study reported in Chapter 4 (see section 4.2.1). As described in section 4.2.1, participants were first shown half of either the male or female faces. Images were presented in a fully randomized order and each image was shown once for 2000ms. In a test phase immediately after the exposure phase, participants were shown all the male or female faces, again in a fully randomized order, and indicated whether or not they had seen each face during the exposure phase. Each face remained onscreen until the participant indicated whether or not they had seen it previously (following Wiese et al., 2014). Which individual faces were shown during the exposure phase was counterbalanced across participants and male and female faces were shown in separate tests. Participants were randomly allocated to either male or female face tests. This part of the study was also run online.

5.2.2 Data analysis

Inter-rater agreement (estimated by Cronbach's alpha) was high for all ratings, with the exception of unhappiness (Cronbach's alpha<.20). At this point, unhappiness was omitted from further analyses. We calculated the average rating for each face separately for each trait by collapsing scores across raters. Descriptive statistics for each trait are shown in Table 5.1, together with results of independent samples t-tests comparing ratings of male and female faces.

Table 5.1 Descriptive statistics for all traits considered in our analyses and results (t and p statistics) for independent samples t-tests for differences between ratings of male and female faces for each trait.

	Male faces			**Female faces**				
Trait	**α**	***M***	***SD***	**α**	***M***	***SD***	***t***	***p***
Aggressiveness	0.90	3.31	0.86	0.80	3.65	0.68	2.18	.032
Attractiveness	0.91	2.77	0.72	0.88	3.03	0.60	1.98	.051
Caringness	0.81	3.58	0.7	0.84	3.37	0.67	-1.52	.132
Commonness	0.79	3.71	0.65	0.71	3.46	0.51	-2.13	.036
Confidence	0.86	3.87	0.69	0.85	3.71	0.72	-1.11	.272
Dominance	0.90	3.44	0.81	0.81	3.45	0.66	0.13	.897
Emotionality	0.65	3.55	0.48	0.64	3.52	0.48	-0.31	.754
Emotional stability	0.84	3.77	0.64	0.71	3.62	0.53	-1.25	.216
Familiarity	0.71	3.64	0.55	0.61	2.76	0.45	-8.72	<.001
Friendliness	0.89	3.40	0.73	0.88	3.42	0.78	0.15	.885
Intelligence	0.78	3.75	0.62	0.70	3.77	0.47	0.23	.821
Meanness	0.75	4.04	0.60	0.82	3.85	0.68	-1.56	.122
Memorability	0.74	3.62	0.64	0.66	3.42	0.47	-1.87	.065
Responsibility	0.84	3.56	0.66	0.69	3.88	0.50	2.73	.008
Sociability	0.91	3.55	0.76	0.84	3.75	0.70	1.37	.173
Trustworthiness	0.84	3.34	0.61	0.77	3.90	0.56	4.73	<.001
Typicality	0.71	3.70	0.56	0.77	3.00	0.51	-6.58	<.001
Weirdness	0.90	4.49	0.83	0.74	4.25	0.58	-1.63	.106

Note. All variables were subsequently standardized within face sex.

Using memory-task responses, we calculated the proportion of participants who correctly identified a face as previously seen (i.e., the hit rate; male faces: M=.76, SD=.09; female faces: M=.76, SD=.09) and the proportion of participants who incorrectly identified a face as previously seen (i.e., the false alarm rate; male faces: M=.21, SD=.12; female faces: M=.24, SD=.12) separately for each image. These were used to calculate d-prime (male faces: M=1.61, SD=0.57; female faces: M=1.50, SD=0.55).

All variables were standardized within face sex (i.e., scores for male faces and scores for female faces were separately converted to z-scores) to control for possible effects of differences in how male and female faces were rated (see Table 5.1). Note that this controls for the possible effects of sex differences in ratings of male and female faces that may have arisen from presenting the male and female stimuli in separate blocks of trials (e.g., the unexpected tendency for female faces to be rated as more aggressive than male faces).

5.3 Results

First, we subjected all ratings to principal component analysis, using no rotation (following, e.g., McAleer et al., 2014; Oosterhof & Todorov, 2008), in order to reduce the traits to orthogonal components. A first component explained approximately 46% of the variance in scores and was highly correlated with trustworthiness and caringness. We labeled this the valence component. A second component approximately 17% of the variance in scores and was highly correlated with dominance and aggressiveness. We labeled this the dominance component. A third component explained approximately 10% of the variance in scores and was highly correlated with rated memorability. We labeled this the rated memorability component. The remaining components each explained only 6% or less of the variance in scores, had no clear interpretation, and were not considered further. The component matrix is shown in Table 5.2. We used these orthogonal components in our main analyses.

Table 5.2 Component matrix for principal component analysis of all traits

Trait	Component 1 (valence)	Component 2 (dominance)	Component 3 (perceived memorability)
Aggressiveness	-0.54	0.77	0.05
Attractiveness	0.77	0.35	0.18
Caringness	0.86	-0.28	0.07
Commonness	0.70	0.23	-0.42
Confidence	0.54	0.59	0.44
Dominance	-0.05	0.87	0.19
Emotionality	0.34	-0.23	0.48
Emotional stability	0.84	0.10	0.14
Familiarity	0.69	0.31	-0.13
Friendliness	0.83	-0.36	0.30
Intelligence	0.64	0.28	-0.14
Meanness	-0.56	0.75	-0.03
Memorability	-0.28	0.03	0.76
Responsibility	0.68	0.20	-0.05
Sociability	0.82	0.06	0.43
Trustworthiness	0.86	-0.26	-0.05
Typicality	0.75	0.16	-0.40
Weirdness	-0.79	-0.28	0.30

Note. We labeled the first component the *valence component* (explained ~46% of the variance in scores), the second component the *dominance component* (explained ~17% of the variance in scores), and the third component the *perceived memorability component* (explained ~10% of the variance in scores).

Hit rate was negatively correlated with the valence component (r=-.27, N=100, p=.007) and positively correlated with the rated memorability component (r=.39, N=100, p<.001). The correlation between hit rate and the dominance component was not significant (r=.03, N=100, p=.787). False alarm rate was positively correlated with the valence (r=.36, N=100, p<.001) and dominance (r=.24, N=100, p=.015) components and negatively correlated with the rated memorability component (r=-.22, N=100, p=.028). The valence component was negatively correlated with d prime (r=-.45, N=100, p<.001), which also tended to be lower for faces scoring high on the dominance component (r=-.19, N=100, p=.062). The rated memorability component and d prime were positively correlated (r=.40, N=100, p<.001). These correlations are plotted in

Figure 5.1. Custom model ANCOVAs including main effects of face sex, the covariate (either the valence, dominance, or rated memorability component), and their interaction showed that none of these relationships were moderated by sex of face (all *p*s>.078).

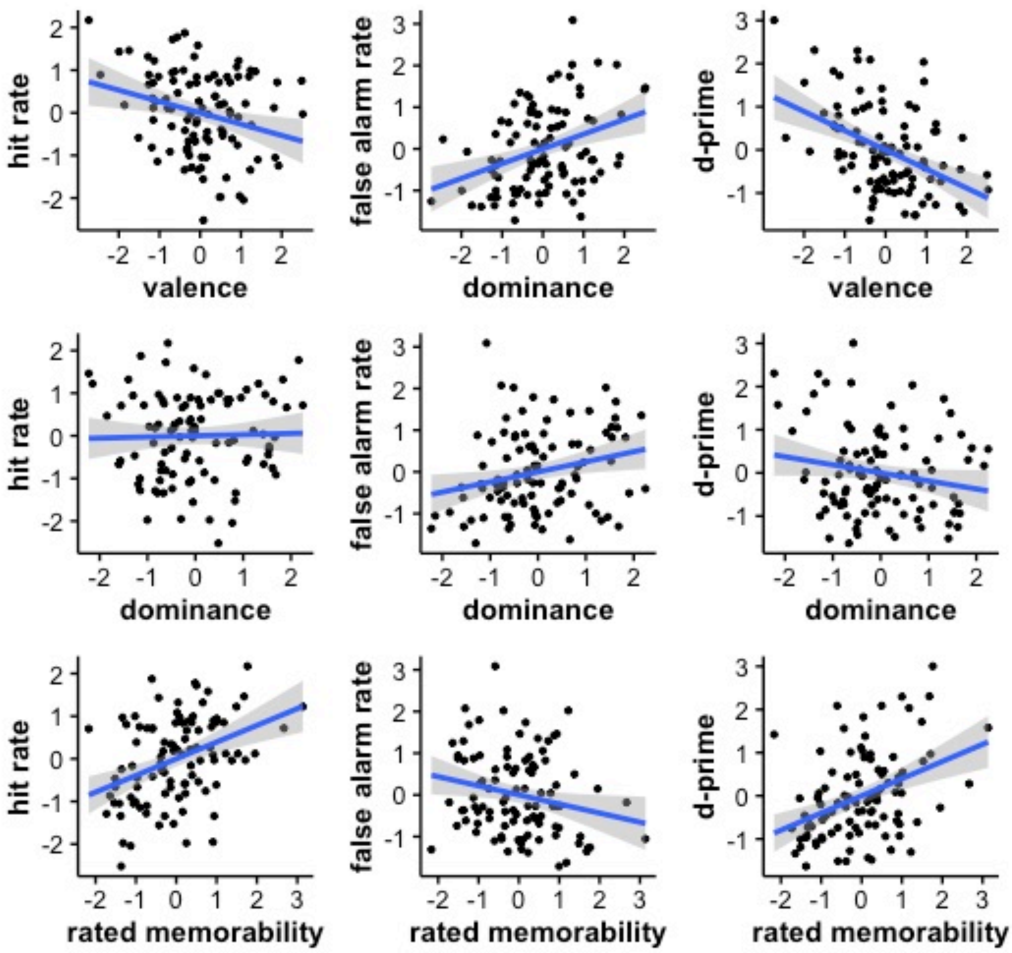

Figure 5.1 Correlations between perceptual components and, hit and false alarm rates, and d-prime.

Additional analyses were conducted on the hit rate, false alarm rate and d-prime using linear regression with valence, dominance, rated memorability components entered as predictors. The regression model on hit rate was significant (F(3,96)=9.40, R^2=0.23, adjusted R^2=0.20). This model revealed significant effects of the valence (beta=-0.27, p= .004) and rated memorability components (beta=0.39, p<.001) while the dominance component did not predict the hit rate significantly (beta=0.03, p=.76). The regression model on false alarm rate was also significant (F(3,96)=9.76, p<.001, R^2=0.23, adjusted R^2=0.21). The false alarm rate was predicted by the valence (beta=0.35, p<.001), dominance (beta=0.24, p=.007), and rated memorability components (beta=0.22, p=.016) respectively. Similarly, the regression model on d-prime was significant ($F(3,96)=20.89$, $p<.001$, $R^2=0.40$, adjusted $R^2=0.38$). The d-prime was predicted by valence (beta=-0.44, $p<.001$), dominance (beta=-0.19, $p=.02$) and rated memorability components (beta=0.40, $p<.001$).

5.4 Discussion

Principal component analysis of the ratings produced three components. These three components reflected the rated valence, dominance, and memorability of the face photographs, respectively. The first two components are similar to those reported by Oosterhof and Todorov (2008), who also found that principal component analysis of ratings of faces for social traits produced two components that were highly correlated with trustworthiness and dominance. We extend Oosterhof and Todorov’s (2008) work by showing that ratings of the memorability of face photographs can be isolated from these valence and dominance components. That typicality loaded strongly onto the valence component is consistent with effects of typicality on trustworthiness reported by Sofer et al. (2014).

Further analyses showed that each of the first three components produced by our principal component analysis predicted the actual memorability of photographs. The valence component was negatively related to d prime, negatively related to hit rate, and positively related to false alarm rate. Faces scoring higher on the dominance component had lower d primes, although this negative correlation was not significant ($p=.062$). The dominance component was not significantly related to hit rate, but was positively related to false alarm rate. The memorability component was positively related to d prime, positively related to hit rate, and negatively related to false alarm rate. Our findings for the memorability component complement studies where memorability ratings were positively related to the actual memorability of face photographs (e.g., Bainbridge et al., 2013; Vokey & Read, 1992). That the valence and dominance components predicted the actual memorability of face photographs complements work suggesting that social traits are important for the memorability of face photographs (Bainbridge et al., 2014; Wiese et al., 2014). We extend this work by demonstrating that the traits that shape the memorability of face photographs can be reduced to valence, dominance, and memorability components, all of which predict the memorability of face photographs.

That the valence component was highly correlated with typicality, attractiveness, and trustworthiness ratings means that lower memorability of images scoring higher on the valence component is consistent with accounts of face recognition that emphasize better memory for atypical faces (Vokey & Read, 1992) and work suggesting that affective processing of faces impairs memory for face photographs (Wiese et al., 2014). Although it is likely that more dominant-looking faces will elicit greater affective processing of faces (because more dominant-looking individuals are perceived as more capable of inflicting physical harm, Oosterhof & Todorov, 2008), it is unclear why the effects of the dominant component appear to be specific to false alarm rates.

Our data demonstrate that valence, dominance, and rated memorability components predict the actual memorability of face photographs. The physical characteristics of faces that covary with the valence or dominance components are now reasonably well understood (see Oosterhof & Todorov, 2008). For example, a subtly smiling demeanor is positively correlated with valence, while brow ridge prominence is positively correlated with dominance. Further work is needed to reveal the physical characteristics that are correlated with the rated memorability component.

Further work is also needed to establish whether the physical characteristics that covary with the valence, dominance, and rated memorability components and predict the memorability of the face photographs shown during the exposure (i.e., learning) phase of the memory task also predict recognition of different photographs of the same individuals shown during the exposure phase. This is a potentially important question, given recent work on the variability of social judgments of individuals from face photographs. Work investigating social judgments of multiple images of the same individuals that used entirely unstandardized images observed greater variability within individuals than between individuals (Jenkins et al., 2011), suggesting that aspects of face images shown during the exposure phase may not necessarily predict recognition of those individuals in different photographs. However, other work that investigated the variability in social judgments of different face photographs of the same individuals using stimuli that varied only in emotional expression observed greater variability between individuals than within individuals (Morrison et al., 2013), suggesting that aspects of face images shown during the exposure phase could predict recognition of those individuals in different photographs under some circumstances. Nonetheless, we do not assume that our results here for pictorial memory of face photographs would necessarily generalize to memory for the faces of unfamiliar individuals.

In summary, we present further evidence that much of the variance in ratings of faces can be explained by valence and dominance components (Oosterhof & Todorov, 2008). However, we also revealed a third component, which primarily reflected ratings of the memorability of face photographs, and showed that all three components contributed to variation in the actual memorability of face photographs. Thus, our analyses present further evidence for the importance of social traits in the memorability of face photographs (Bainbridge et al., 2013) and, perhaps more importantly, clarify the components underlying traits that predict the memorability of face photographs. Nonetheless, although social traits predict the memorability of face photographs, most of the variance in the memorability of face photographs remained unexplained, highlighting the need to develop new approaches to the study of face photograph memorability.

Chapter 6

General Discussion

Previous research has identified several facial cues to physical attractiveness, such as symmetry, averageness, sexual dimorphism, and skin characteristics. Although several lines of evidence suggest that physically attractive faces have motivational salience (e.g., Aharon et al., 2001; Bzdok et al., 2011), little was known about factors that influence the motivational salience of facial attractiveness. In Chapter 2, I investigated the effects of women's hormone levels on the motivational salience of facial attractiveness. To address this issue, I investigated the relationships between within-subject changes in women's salivary hormone levels (estradiol, progesterone, testosterone, and estradiol-to-progesterone ratio) and within-subject changes in the motivational salience of attractiveness in male and female faces. The results suggest that the motivational salience of facial attractiveness is modulated by within-woman changes in testosterone levels and, to a lesser extent, estradiol-to-progesterone ratios. Specifically, the effect of attractiveness on the motivational salience of faces was greater in test sessions where women had higher testosterone levels. Additionally, the motivational salience of attractive female faces was greater in test sessions where women had high estradiol-to-progesterone ratios.

A key result from Chapter 2 was that motivational salience of faces is generally positively correlated with their physical attractiveness. This is consistent with results of previous studies (Levy et al., 2008; Hahn et al., 2013, 2014, 2015). Chapter 3 builds on these findings by examining whether physical characteristics other than attractiveness contribute to the motivational salience of facial attractiveness. Research with male macaques has shown that more dominant macaques' faces hold greater motivational salience (Deaner, Khera, & Platt, 2005). In Chapter 3, I investigated whether perceived dominance also contributed to the motivational salience of faces in human participants. Principal component analysis of third-party ratings of faces for multiple traits revealed two orthogonal components. The first component ("valence") was highly correlated with rated trustworthiness and attractiveness. The second component ("dominance") was highly correlated with rated dominance and aggressiveness. Importantly, both components were positively and independently related to the motivational salience of faces, as assessed from responses on a standard key-press task. The two-component structure underlying perceptions of faces (valence and dominance components is consistent with previous research (Oosterhof & Todorov, 2008).

While the work reported in Chapter 2 investigated *within*-woman changes in the motivational salience of facial attractiveness, Chapter 4 investigated possible *between*-woman differences in responses to facial attractiveness. As several researchers have proposed that partnership status influences women's perception of attractiveness (Karremans et al., 2011; Ritter et al., 2010), in Chapter 4 I tested whether the effect of attractiveness on women's response differed as a function of their romantic partnership status. Consistent with previous research, women's memory was poorer for face photographs of more attractive men and more attractive men's faces held greater motivational salience. However, in neither study were the effects of attractiveness modulated by women's partnership status or partnered women's reported commitment to or happiness with their romantic relationship. These results do not support the proposal that partnered women discriminate potential alternative mates along the physical attractiveness dimension less than unpartnered women do.

A key result from Chapter 4 was that more attractive faces were harder to remember. Building on this result, Chapter 5 investigated the characteristics contributing to the memorability of face photographs. While some traditional work on memorability of face photographs emphasizes importance of typicality, familiarity, and memorability ratings (e.g., Vokey & Read, 1992), more recent work suggests that ratings of social traits also predict the memorability of face photographs independently of typicality, familiarity, and memorability ratings (Bainbridge et al., 2013). However, what components underlie these traits is unclear, as well as how these components relate to the actual memorability of face photographs. Principal component analysis of all these face ratings produced three orthogonal components that were highly correlated with trustworthiness, dominance, and memorability ratings, respectively. Furthermore, each of these orthogonal components also predicted the actual memorability of face photographs.

In the remaining section, I will discuss some issues raised by the results presented in the previous four chapters, as well as the limitations of the current work and possible directions for future research.

6.1 Testosterone and motivational salience

The work reported in Chapter 2 suggests that fluctuations of women's testosterone levels modulate the motivational salience of facial attractiveness. It remains unclear if the effects of testosterone on the motivational salience of facial attractiveness among naturally cycling women generalize to women who are pregnant, postpartum, or taking hormonal contraceptives. Indeed, there is evidence showing that hormonal changes induced by pregnancy, postpartum and hormonal contraceptives use could affect women's facial preferences (e.g., Cobey, Little, & Roberts, 2015; Jones et al., 2005; Little, Burriss, Petrie, Jones, & Roberts, 2013; Little, Jones, Penton-Voak, Burt, & Perrett, 2002). Further research is also needed to examine whether this effect of women's testosterone on the motivational salience of facial attractiveness can be replicated in men. Furthermore, only faces were used as stimuli in Chapter 2. Further research is also needed to examine whether this effect of testosterone on the motivational salience of social incentives, i.e. faces, can generalizes to other incentives, such as monetary rewards, or also occurs for other types of social incentives (e.g., voices, bodies, etc.).

6.1.1 Sex differences in the relationships between testosterone and motivational salience?

Previous research has suggested a positive link between testosterone and aggression in man (Archer, 2006), which is thought to promote the pursuit of high status or social dominance (Eisenegger, Haushofer, & Fehr, 2011). Furthermore, Roney (2016) provided a theoretical framework for the role of testosterone in man. In this model, testosterone will shift the individual's investments of resources from survival efforts to mating efforts. Inputs from the environments, such as the presence of potential mates, will induce the production of testosterone while other cues, such as food shortage or illness, will inhibit the production of testosterone (Roney, 2016). As a result, testosterone promotes intra-sexual competition but suppresses the immune function or fat storage (Roney, 2016).

There are findings suggesting a positive link between testosterone and reward sensitivity in men, leaving open the possibility that the findings observed in women may replicate in men. For instance, studies of hypogonadal patients found that higher levels of testosterone in men is associated with stronger activations in reward circuit, such as orbitofrontal cortex and the insula, in response to the visual sexual stimuli (Redouté et al., 2005). Similarly, Op de Macks et al. (2011) found that testosterone levels positively correlated with activations in the ventral striatum, a brain region in the reward circuit, during processing of monetary incentives in both boys and girls. Moreover, a longitudinal study revealed a within-man association between high testosterone and high reward dependence (Määttänen et al., 2013). Reward dependence is thought to measure the importance of social rewards to the individual (Cloninger, 1987). Taken together, these findings show a positive correlation between testosterone and sensitivity to reward, suggesting that the effects of testosterone may only differ in size across sexes rather the direction.

However, there is research suggesting sex differences may occur in the effects of testosterone on the motivational salience of facial attractiveness. Research investigating the relationship between testosterone and inter-temporal choice in both sex found a positive correlation between testosterone concentrations and delay-discounting rates in women and a negative correlation in men (Doi, Nishitani, & Shinohara, 2015). Delay discounting is the fact that humans discount the subjective evaluation of a reward according to the delay in the reward delivery (e.g., Green & Myerson, 2004). Doi et al. (2015) proposed that this sex difference might be due to the curvilinear effect of testosterone. Indeed, previous research also found a curvilinear / nonlinear relationship between testosterone levels and spatial cognition tasks (Moffat & Hampson, 1996). Moreover, the studies suggesting a similar pattern of results across both sex in the relationship between testosterone and reward sensitivity used either adolescent males (Op de Macks et al., 2011) or hypogonadal patients (Redouté et al., 2005). The results of these findings might not be able to generalize to normal adult men, as normal adult men's testosterone levels should be higher. Taken together, the positive correlations between testosterone levels and the motivational salience of facial attractiveness observed in women might not be able to be replicated in men.

6.1.2 Testosterone and other types of incentives

Chapter 2 suggests that women's testosterone levels modulate the motivational salience of facial attractiveness. Whether women's testosterone levels would modulate the motivational salience of other types of incentives remains unclear.

Hahn, DeBruine, Fisher, and Jones (2015) using a similar research design as Chapter 2 found that testosterone levels also modulated the motivational salience of infant cuteness. They found that women would make more effect to view images of cute infant faces when their testosterone levels were high. This pattern of results, together with the studies reported in Chapter 2, suggest the role of testosterone in responses to the motivational salience of social incentives.

However, it is less clear whether within-individual changes in women's testosterone levels modulate the incentive salience of incentives other than social incentives, such as financial incentives. Research investigating the effects of exogenous testosterone found the positive effect of testosterone administration on the enhanced activation in the brain regions implicated in motivation and reward processing in response to the financial incentives (Hermans et al., 2010; van Honk et al., 2004). Further work is needed to examine the effects of exogenous testosterone on the financial incentives also replicate women whose hormone fluctuations occur naturally.

6.2 Valence and memorability of face photographs

Result from Chapter 4 suggests that more attractive faces were harder to remember. Chapter 5 extended this result by suggesting that valence dimension, which is highly correlated with trustworthiness and attractiveness ratings, predicts the memorability of face photographs. More specifically, faces scoring higher on the valence dimension were harder to remember.

This pattern of results is consistent with early research emphasizing better memory for atypical faces (Vokey & Read, 1992) as the valence component was highly correlated with typicality ratings. Moreover, this pattern of results is also consistent with recent work suggesting that affective processing of faces impairs memory for face photographs (Light, Hollander, & Kayra-Stuart, 1981; Wiese et al., 2014).

That faces scoring higher on the valence dimension were harder to remember is also consistent with the literature into the “cheater detection module”, which suggests a memory advantage for the faces of cheaters (Bayliss & Tipper, 2006; Mealey, Daood, & Krage, 1996; Oda, 1997). While some studies using verbal descriptions to convey information of trustworthiness, research using rated facial trustworthiness suggests a similar pattern of results (Rule, Slepian, & Ambady, 2012; Tsukiura, Shigemune, Nouchi, Kambara, & Kawashima, 2013).

However, there are a number of studies finding different patterns of results. For example, research has found that perceived facial attractiveness is associated with better recognition performance (Cross, Cross, & Daly, 1971; Marzi & Viggiano, 2010) or no significant relationships between facial attractiveness and memory for faces (e.g., Wickham & Morris, 2003). Literature into the relationship between trustworthiness and memory for faces also suggests that when confounding variables have been controlled, such as the rarity of untrustworthy faces (Barclay, 2008), the memory advantage for untrustworthy faces will disappear (e.g., Mehl & Buchner, 2008).

There are several possible explanations for the mixed pattern of results. First, there are considerable variations in the methods used in the previous research examining the relationships between attractiveness / trustworthiness and memory for faces. For example, participants were asked to rate on facial characteristics, such as attractiveness, trustworthiness or typicality, during the learning phase in some studies (Cross et al, 1971; Light, et al., 1981; Marzi & Viggiano, 2010; Sarno & Alley, 1997; Shepherd & Ellis, 1973) while participants were only instructed to view the faces without any tasks in other studies (e.g., Rule et al., 2012). Asking participants to rate on a specific trait during learning phase may lack ecological validity and cause a different pattern of results (Rule et al., 2012). Similarly, different length of retention interval between learning phase and testing phase has been used in previous studies and may also contribute to the different effects of attractiveness / trustworthiness on the memory (e.g., Light, et al., 1981; Shepherd & Ellis, 1973).

Second, the mixed evidence across studies may be partly due to other facial characteristics, which were not controlled in previous studies. For example, distinctiveness has been demonstrated to affect face memorability (e.g., Valentine, 1991) and has not been controlled in most studies investigating the relationship between facial attractiveness and memorability. Similarly, the frequency of one kind of face presented during the learning phase might also affect the memory performance (Barclay, 2008). Furthermore, studies discussed above used face stimuli varied a lot in many ways. Using un-standardized photos of faces, such as photographic portraits from high school yearbooks (e.g., Cross et al., 1971; Light et al., 1981), may result in unreliable results. Having not controlled these potential confounding variables might partly account for the different patterns of results. Finally, as some studies suggests a curvilinear relationship between attractiveness and face memorability (Shepherd & Ellis, 1973), it is important to sample a full range of values on attractiveness or trustworthiness to get reliable results.

6.3 Cross-cultural agreement and differences

While study presented in Chapter 2 was run in the laboratory, studies presented in Chapter 3 to Chapter 5 were run online. As the studies were run in the UK, most of our participants were from the UK or Western society. Although early research investigating facial attractiveness has suggested that there is much agreement on general judgments of facial attractiveness across different cultures (e.g. Cunningham et al. 1995), systematic variations in facial preferences have been observed across cultures recently (Honekopp, 2006; Penton-Voak, Jacobson, & Trivers, 2004; Scott, Clark, Josephson, Boyette, Cuthill, & Fried et al., 2014). Indeed, most research in this field uses Western, educated, industrialized, rich and democratic (WEIRD) participants who are arguably not representative of other societies or populations (Henrich, Heine, & Norenzayan, 2010a, 2010b). Further research using cross-cultural samples is needed to generalize the finding of current studies to human populations.

Cross-cultural research not only provides us with a broader view of human mating behaviour but also allows us to test evolutionary theories that try to reveal the mechanisms underlying the behaviour. Evolutionary psychologists have been using cross-cultural samples to test the evolution-based hypotheses, as they believe the cross-cultural variations could due to adaptations to environments (Buss, 1989). Although facial cues to facial attractiveness discussed in Chapter 1 were mostly identified by research using WEIRD populations, efforts have been made to test these findings across cultures. Next, I will review the cross-cultural research in facial attractiveness as well as the theories explaining the agreement and variation across different cultures.

6.3.1 Symmetry

Two early studies examined preferences for symmetrical faces in non-western cultures, Japanese, Brazilian and Indian (Jones & Hill, 1993; Kowner, 1996). However, the results from their studies may not be reliable due to the problems in stimuli or methodology (Rhodes, Roberts et al., 1999). More recent research using modern computer graphic techniques to manipulate face suggests that preferences for symmetric Japanese faces have been observed among Japanese students (Rhodes et al., 2001). Little, Apicella, and Marlowe (2007) explored symmetry preference among participants from UK and Hadza. The Hadza is a hunter-gatherer society from Tanzania in East Africa and the Hadza locals live in a harsh environment comparing to British people (Little et al., 2007). Both British and the Hadza participants preferred symmetrical opposite-sex faces of both British and Hadza faces. However, the Hadza participants showed stronger preferences for facial symmetry than British participants in general.

Evolutionary psychologists propose that facial symmetry is attractive because symmetry signals mate quality (e.g., Thornhill & Gangestad, 1999, Thornhill & Møller, 1997). Other researchers, however, propose that symmetry is preferred simply because symmetry is easier to process (e.g., Reber, Schwarz, & Winkielman, 2004). Consistent with the evolutionary view, the stronger preference for symmetry in Hadza may be due to the challenging environment (i.e. high load of pathogens). And that the Hadza showed no differences in their symmetry preferences between UK and Hadza faces suggests that the visual experience does not account for the increased preference for symmetry.

6.3.2 Averageness

Early work investigating the preferences for facial averageness within and between five cultural groups (Brazilians, U.S. Americans, Russian, Ache Indians, Hiwi Indians) only found the averageness preference in Ache Indians (Jones & Hill, 1993). That they failed to replicate the well-documented preferences for facial averageness in Western populations suggests the findings from their studies might not be reliable (Rhodes, 2006). Rhodes et al. (2001) tested the averageness preferences in both Chinese and Japanese populations. Their results confirmed the averageness preferences in both cultural groups. Apicella, Little, and Marlowe (2007) tested the averageness preferences in the Hadza and Western participants. They reported the preferences for average opposite-sex faces within their own culture in both populations. Interestingly, while Western participants preferred averageness in both European and Hadza faces, the Hadza only preferred averageness in faces of their own race (Apicella et al., 2007).

Research discussed above suggests the preferences for averageness in face has been observed across cultures. That the Hadza participants only preferred the average faces of their own-race but not European faces suggests the role of visual experience in the averageness preferences. Since the Hadza people have limited exposure to European faces, they may not have enough visual experience to form a mental representation of average European faces (Apicella et al., 2007).

6.3.3 Sexual dimorphism

While femininity in female faces is consistently associated with attractiveness, there are more variations in the preferences of masculinity in male faces even within Western society (see Rhodes, 2006 for a review). Research using Western population suggests that men show stronger preferences for femininity in female faces when they reported higher sexual desire (Jones, Little, Watkins, Welling, & DeBruine, 2011), when their testosterone levels were high (Welling et al., 2008) or when they were exposed to visual cues of pathogen contagion (Little, DeBruine, & Jones, 2011). Similarly, research suggests that Western women show stronger preferences for masculinity in male faces when their conception risks were high (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999), when they were considering short-term relationships than long-term relationships (Burt et al., 2007; Penton-Voak et al., 1999, 2003; Little et al., 2002), when they were exposed to visual cues of pathogen contagion (Little et al., 2011), when they were more sensitive to pathogen disgust (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010), or when they perceived themselves as more attractive than average (Little, Burt, Penton-Voak, & Perrett, 2001).

6.3.3.1 Femininity in female faces

Perrett et al. (1998) investigating preferences for female femininity in both Japanese and British participants showed both groups of participants prefer female femininity in Japanese and British faces, particularly for own-race faces. Penton-Voak et al. (2004) investigated men’s preferences for femininity in female faces in Jamaican and British participants. They found that Jamaican men preferred more masculine female faces overall than British men do. However, they still preferred feminized female faces of their own population (Penton-Voak et al., 2004). Marcinkowska et al. (2014) investigating men's preferences for femininity in female faces across 28 countries also found a similar pattern of results. While men preferred feminized female faces in general, the degree to which femininity is preferred in female faces is related to the health of the country (as measured by national health index). Men's preferences for facial femininity increased as health increased (Marcinkowska et al., 2014).

These results suggest that preferences for female femininity tend to be stronger in regions with better health conditions while preferences for female femininity tend to be weaker in harsh environments. This pattern of results does not support the hypothesis that femininity will be more valued in harsh environments as femininity signal mate quality (e.g., Thornhill & Gangestad, 1999). As femininity is also associated with lower perceived dominance (Perrett et al., 1998), it is proposed that in harsh environments men prefer cues to effective resource acquisition rather than high reproductive success (Marcinkowska et al., 2014).

6.3.3.2 Masculinity in male faces

Early work investigating women's preferences for male facial masculinity cross cultures did not find differences in masculinity between Japanese and British participants (Perrett et al., 1998). Both populations preferred feminized to average or masculinized shapes of male faces. Penton-Voak et al. (2004) comparing women's preferences for male masculinity between British and Jamaican samples found that Jamaican women preferred more masculine male faces than British women did. Similarly, DeBruine, Jones, Crawford, Welling, and Little (2010) investigating women's preference for masculinized male faces across 30 countries found that the degree to which male masculinity was preferred was related to the health of the country. Women's preferences for facial masculinity increased as health decreased (DeBruine et al., 2010).

That women's preferences for male facial masculinity increase as health decreased supports the trade-off hypothesis in which women trade off between good genes and good parenting (Gangestad & Simpson, 2000; Gangestad & Thornhill, 2008). According to the trade-off theory, women prefer more masculinized male faces when good genes become more important. As a result, women's preferences for male masculinity increased as health decreased (DeBruine et al., 2010). Scott et al., (2004), however, found an opposite pattern of results which suggested that masculinity preferences were negatively related to disease burden.

6.3.4 Skin colouration

Skin characteristics also play an important role in attractiveness judgments independently of facial shapes (Jones et al., 2004). Research using Western samples demonstrates that increasing facial redness (a*), yellowness (b*) and lightness (L*) increases facial attractiveness (Re et al., 2011; Stephen, Oldham, et al., 2012; Stephen, Scott, et al., 2012) and perceived health (Stephen, Coetzee et al., 2009, 2011; Stephen, Law Smith, et al., 2009). Research using African samples reported a parallel pattern of results (Stephen, Coetzee et al., 2009, 2011; Stephen, Scott, et al., 2012) (Coetzee et al., 2012). Their results suggest that increasing facial yellowness and lightness also increases attractiveness in Africans. However, some studies failed to find the association between redness and attractiveness (Coetzee et al, 2012, Stephen, Scott, et al., 2012).

Facial colouration is proposed to signal individual health condition. Facial redness is thought to reflect blood oxygenation (Stephen, Coetzee, et al., 2009) or women's fertility (Jones et al., 2015). Facial yellowness is thought to reflect individual's consumption of fruits and vegetables (Stephen, Coetzee, et al., 2011). While much agreement has been found in facial colouration preference between African and European samples, studies using other cultural samples are needed to test these hypotheses.

In summary, there are both agreement and variation in facial attractiveness judgments across different cultures. Although most the findings of facial attractiveness have been build on studies using Western samples, there is a growing body of cross-cultural research that attempts to reveal facial preferences of other cultural populations. Researchers may benefit from more cross-cultural research by exploring the possible reasons accounting for the variations in facial attractiveness judgments.

6.4 Conclusions

Attractive faces hold motivational salience and are harder to remember. Both within-woman and between-women variations might influence women's response to facial attractiveness. This thesis demonstrated that within-woman variables, such as fluctuations in hormone levels, influenced the motivational salience of facial attractiveness. However, the between-women variable romantic relationship status did not appear to modulate women's responses to facial attractiveness. In addition to attractiveness, dominance also contributed to both the motivational salience and memorability of faces. This latter result demonstrates that, although attractiveness is an important factor for the motivational salience of faces, other factors might also cause faces to hold motivational salience.

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Supplemental Materials (Chapter 2)

Results of linear mixed models, using lme4 and lmerTest in R (REML = false)

kp	= key press score
estradiol	= estradiol (centered) in pg/mL
progesterone	= progesterone (centered) in pg/mL
testosterone	= testosterone (centered) in pg/mL
e_to_p_ratio	= estradiol-to-progesterone ratio (centered)
att	= face attractiveness rating (centered) (0-7)
sexdim	= face sexual dimorphism rating (centered) (0-7)
face_sex	= sex of face (0 = female, 1 = male)
face_sex_rev	= sex of face (0 = male, 1 = female) [used in reversed analyses to interpret interactions with face_sex]

ATTRACTIVENESS (att) - FULL MODEL (face_sex: 0 = female, 1 = male)

```
Formula: kp ~ 1 + att * face_sex * progesterone
                + att * face_sex * estradiol
                + att * face_sex * testosterone
                + att * face_sex * e_to_p_ratio
                + (1 | participant/session) + (1 | face) + (1 | participant:face)

Random effects:
 Groups              Name        Variance Std.Dev.
 participant:face    (Intercept) 68.195   8.258
 session:participant (Intercept)  9.530   3.087
 face                (Intercept)  4.692   2.166
 participant         (Intercept) 40.101   6.333
 Residual                        92.785   9.632
Number of obs: 25000, groups: participant:face, 5000; session:participant, 250; face, 100; participant, 50

Fixed effects:
                                Estimate    Std. Error            df t value Pr(>|t|)
(Intercept)                   -4.8749539     0.9844048    62.0000000  -4.952 5.88e-06 ***
att                            4.9831253     0.5286644    99.0000000   9.426 1.78e-15 ***
face_sex                       0.0003114     0.5078591    99.0000000   0.001   0.9995
progesterone                  -0.0014927     0.0031785   245.0000000  -0.470   0.6390
estradiol                     -0.0189562     0.2507328   257.0000000  -0.076   0.9398
testosterone                   0.0443055     0.0170927   273.0000000   2.592   0.0101 *
e_to_p_ratio                  -2.0703588    10.2941309   252.0000000  -0.201   0.8408
att:face_sex                   1.2335166     0.7847023    99.0000000   1.572   0.1191
att:progesterone              -0.0014961     0.0018286 23026.0000000  -0.818   0.4133
face_sex:progesterone          0.0010146     0.0017566 23026.0000000   0.578   0.5635
att:estradiol                 -0.1107348     0.1369595 24593.0000000  -0.809   0.4188
face_sex:estradiol             0.0462959     0.1315695 24593.0000000   0.352   0.7249
att:testosterone               0.0491223     0.0086043 19890.0000000   5.709 1.15e-08 ***
face_sex:testosterone         -0.0101192     0.0082657 19890.0000000  -1.224   0.2209
att:e_to_p_ratio              13.9555314     5.7402745 24521.0000000   2.431   0.0151 *
face_sex:e_to_p_ratio          8.0614316     5.5143691 24521.0000000   1.462   0.1438
att:face_sex:progesterone      0.0009621     0.0027142 23026.0000000   0.354   0.7230
att:face_sex:estradiol         0.1100923     0.2032905 24593.0000000   0.542   0.5881
att:face_sex:testosterone     -0.0165061     0.0127715 19890.0000000  -1.292   0.1962
att:face_sex:e_to_p_ratio    -18.8960257     8.5203521 24521.0000000  -2.218   0.0266 *
```

ATTRACTIVENESS (att) - REDUCED MODEL (face_sex: 0 = female, 1 = male)

```
Formula: kp ~ 1 + progesterone   + estradiol
                + att * testosterone
                + att * face_sex * e_to_p_ratio
                + (1 | participant/session) + (1 | face) + (1 | participant:face)

Random effects:
 Groups              Name        Variance Std.Dev.
 participant:face    (Intercept) 68.314   8.265
 session:participant (Intercept)  9.530   3.087
 face                (Intercept)  4.689   2.166
 participant         (Intercept) 40.100   6.332
 Residual                        92.778   9.632
Number of obs: 25000, groups: participant:face, 5000; session:participant, 250; face, 100; participant, 50

Fixed effects:
                                Estimate    Std. Error            df t value Pr(>|t|)
(Intercept)                   -4.8749539     0.9843944    62.0000000  -4.952 5.88e-06 ***
progesterone                  -0.0010032     0.0030544   209.0000000  -0.328 0.742894
estradiol                      0.0021495     0.2419248   223.0000000   0.009 0.992919
att                            4.9831253     0.5286642    99.0000000   9.426 1.78e-15 ***
testosterone                   0.0395520     0.0165841   242.0000000   2.385 0.017853 *
face_sex                       0.0003114     0.5078589    99.0000000   0.001 0.999512
e_to_p_ratio                  -1.4115245    10.1942846   242.0000000  -0.138 0.889990
att:testosterone               0.0399667     0.0059970 20013.0000000   6.664 2.73e-11 ***
att:face_sex                   1.2335166     0.7847020    99.0000000   1.572 0.119149
att:e_to_p_ratio              16.2476138     4.9151158 24650.0000000   3.306 0.000949 ***
face_sex:e_to_p_ratio          6.7019492     4.7167688 24649.0000000   1.421 0.155365
att:face_sex:e_to_p_ratio    -20.0236256     7.2879653 24649.0000000  -2.747 0.006010 **
```

ATTRACTIVENESS (att) - REDUCED MODEL REVERSED (face_sex_rev: 0 = male, 1 = female)

```
Formula: kp ~ 1 + progesterone   + estradiol
                + att * testosterone
                + att * face_sex_rev * e_to_p_ratio
                + (1 | participant/session) + (1 | face) + (1 | participant:face)

Random effects:
 Groups              Name        Variance Std.Dev.
 participant:face    (Intercept) 68.314   8.265
 session:participant (Intercept)  9.530   3.087
 face                (Intercept)  4.689   2.166
 participant         (Intercept) 40.100   6.332
 Residual                        92.778   9.632
Number of obs: 25000, groups: participant:face, 5000; session:participant, 250; face, 100; participant, 50

Fixed effects:
                                     Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                        -4.875e+00  9.844e-01  6.200e+01  -4.952 5.89e-06 ***
progesterone                       -1.003e-03  3.054e-03  2.090e+02  -0.328  0.74289
estradiol                           2.149e-03  2.419e-01  2.230e+02   0.009  0.99292
att                                 6.217e+00  5.799e-01  9.900e+01  10.720  < 2e-16 ***
testosterone                        3.955e-02  1.658e-02  2.420e+02   2.385  0.01785 *
face_sex_rev                       -3.114e-04  5.079e-01  9.900e+01  -0.001  0.99951
e_to_p_ratio                        5.290e+00  1.019e+01  2.430e+02   0.519  0.60427
att:testosterone                    3.997e-02  5.997e-03  2.001e+04   6.664 2.73e-11 ***
att:face_sex_rev                   -1.234e+00  7.847e-01  9.900e+01  -1.572  0.11915
att:e_to_p_ratio                   -3.776e+00  5.390e+00  2.465e+04  -0.701  0.48362
face_sex_rev:e_to_p_ratio          -6.702e+00  4.717e+00  2.465e+04  -1.421  0.15537
att:face_sex_rev:e_to_p_ratio       2.002e+01  7.288e+00  2.465e+04   2.747  0.00601 **
```