

THE ROLE OF MALE SECONDARY SEXUAL TRAITS IN  
HUMAN MATE CHOICE: ARE THEY PREFERRED BY  
FEMALES AND DO THEY SIGNAL MATE QUALITY?

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## **ABSTRACT.**

Judgements of physical attractiveness are thought to reflect evolved preferences for a high quality mate. The central aim of this thesis was to investigate the hypothesis that female preferences are adaptations for finding good quality mates and that faces and bodies signal honest information about mate quality. To date, most human mate preference studies have examined face or body attractiveness alone, and many have created stimuli using computer graphic techniques. Throughout these studies, I endeavoured to maximise the biological relevance of my studies by incorporating both face and body attractiveness, and using photographs of individual participants.

Most research on attractiveness has focused on faces or bodies separately, while our preferences have evolved based on both seen together. A fundamental requirement of studying face and body attractiveness independently is that there is no interaction between the two. My first study confirmed that the face and body did not interact when an overall attractiveness judgment was made. I also investigated the independent contributions of rated attractiveness of the face and the body to ratings of overall attractiveness. Face and body attractiveness each made significant independent contributions to overall attractiveness in males and females. For both sexes, facial attractiveness predicted overall attractiveness more strongly than did body attractiveness, and this difference was significant in males. My results validate the assumption that studying faces and bodies separately in the context of mate choice will produce biologically meaningful results, and suggest that face and body attractiveness may convey potentially independent signals about an individual's mate quality.

The next three studies were based on data collected from one large sample of adult, heterosexual, caucasian males. Each male was photographed, completed a sexual history and lifestyle questionnaire, and provided a saliva sample (for testosterone assay) and a semen sample. All ratings of these face and body photographs were made by heterosexual, caucasian females in order to capture male attractiveness in a mate choice context.

Studies of women's preferences for male faces and bodies have revealed an increase in visual preferences for masculine and symmetric men at the fertile point of the menstrual cycle. However, cyclic shifts in visual preferences have only been shown in studies that require female choices to be made between subtle variants of the same

computer-generated identity. These methods, while being very sensitive to small shifts in female preferences, do not necessarily capture functional female responses that subsequently influence mate-choice. I collected attractiveness ratings of unmanipulated male face and body photographs from 25 normally cycling women at high and low fertility days of the menstrual cycle. These attractiveness ratings were then correlated with masculinity and symmetry ratings provided by independent sets of raters. Using this method, I found no evidence for any shift in female preferences over the menstrual cycle. There was no significant difference between high and low fertility ratings of attractiveness. Furthermore, correlations between attractiveness and masculinity, and attractiveness and symmetry did not differ significantly between high and low fertility phases of the cycle. This study suggests that a menstrual cycle shift in preferences may be too subtle to detect in photographs of real faces and bodies. My results highlight the importance of studying human mate choice under realistic conditions to maximise the biological relevance of the findings.

The psychological mechanisms underlying attractiveness judgements in humans are thought to be evolved adaptations for finding a high quality mate. The third and fourth studies presented in this thesis thus investigated two potential aspects of mate quality in men: testosterone and semen quality. Testosterone (T) is important for the development of secondary sexual characteristics, but it imposes significant physiological costs that are thought to make the expression of T-dependent traits an honest signal of mate quality. Recent research has shown that men with one current partner have lower T than men reporting multiple current partners. These high-T, multiple partnered men may therefore have a reproductive advantage over their low-T counterparts via increased lifetime mating success. I directly addressed this hypothesis and extended prior research by investigating whether T is associated with a) lifetime mating success and b) attractiveness and masculinity, in a sample of 119 males. I found a significant positive correlation between T and mating success. There was, however, no correlation between T and rated masculinity or attractiveness. This study indicates that although current levels of T covary with male mating success, this effect may not be mediated by women's preferences for visual cues to T levels conveyed in static face or body features.

The fourth study in this thesis investigated the phenotype-linked fertility hypothesis, which proposes that females obtain reliable information on male fertility from male expression of sexual traits. A previous study of Spanish men reported that

facial attractiveness was positively associated with semen quality. I aimed to determine whether this effect was widespread by examining a large sample of Australian men. I also extended my study to determine whether cues to semen quality are provided by components of attractiveness: masculinity, averageness, and symmetry. I found no significant correlations between semen quality parameters and attractiveness or attractive traits. While male physical attractiveness may signal aspects of mate quality, my results suggest that phenotype-linked cues to male fertility may not be generalised across human populations.

Together, these studies challenge current methodologies and theories of preferences for secondary sexual traits as honest signals of mate quality. The findings show that it is important to study human mate preferences in biologically relevant contexts, for example by using photographs of both faces and bodies, to maximise the real life application of results. In addition, the findings suggest that male attractiveness does not signal cues to testosterone or semen quality, although testosterone is associated with mating success. The implications of these findings and possible avenues for future research are discussed.

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## MANUSCRIPTS FOR PUBLICATION.

This thesis is submitted as a series of discrete manuscripts. The following manuscripts have been submitted to international journals:

- I. Peters, M., Rhodes, G, & Simmons, L. W. (2007) Contributions of the face and body to overall attractiveness. *Animal Behaviour*, **73**, 937-942.
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- III. Peters, M., Rhodes, G, & Simmons, L. W. (2008) Does attractiveness in men provide clues to semen quality? *Journal of Evolutionary Biology*, **21**, 572-579.
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All manuscripts were written in collaboration with Leigh Simmons and Gillian Rhodes. For each experiment, I was the main contributor and responsible for the experimental design, data collection, statistical analyses and writing. Leigh Simmons and Gillian Rhodes contributed to the experimental design, statistical analyses and writing.

Author contributions to each manuscript: I MP = 80 %, LWS = 10 %, GR = 10 %; II MP = 90 %, LWS = 5 %, GR = 5 %; III MP = 80%, LWS = 10 %, GR = 10 %; IV MP = 80 %, LWS = 10 %, GR = 10%.

Each author has given permission for all work to be included in this thesis.

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# **CHAPTER ONE**

## **GENERAL INTRODUCTION.**

# CHAPTER ONE: GENERAL INTRODUCTION.

## 1.1 PREFERENCES FOR SECONDARY SEXUAL CHARACTERISTICS MAY BE ADAPTATIONS FOR DETECTING HIGH QUALITY MATES.

Darwin (1871) proposed that male secondary sexual characteristics (sexually dimorphic traits not directly involved with reproduction) evolved because they give some individuals a reproductive advantage over others, either through intimidation of rivals or via a female preference to mate with males displaying these traits. Therefore, as a result of sexual selection, males in both human and non-human species often show greater development of secondary sexual characteristics than do females (Darwin, 1871; Bateman, 1948; Trivers, 1972). Examples of secondary sexual traits include the peacock's train, bright coloration in birds and fishes, and a large chin, jaw and brow ridge in human male faces (Andersson, 1994).

Secondary sexual characteristics require costly resources to develop, and only the fittest individuals may be able to afford to display them (Zahavi, 1975). Many studies have shown that the presence of these traits is attractive in human male faces and bodies (Rhodes, 2006). Human perceptions of face and body attractiveness may therefore reflect preferences for fitness in a potential mate. If human mate preferences for secondary sexual traits are psychological adaptations for finding a good quality mate (Barber, 1995; Thornhill & Gangestad, 1999) then both the preference (attractiveness) and the signal (secondary sexual traits) should be reliably associated with direct measures of mate quality.

There are good reasons to believe that secondary sexual characteristics may honestly signal mate quality. The Hamilton-Zuk Hypothesis of Sexual Selection proposes one possible mechanism that may generate heritable variation in fitness associated with secondary sexual traits. According to this model, the expression of certain male traits may be associated with parasite or pathogen resistance. Females may use these heritable fitness cues when choosing a mate. The co-evolution of the preference and parasite resistance will lead to the exaggeration of male traits that signal fitness (Hamilton & Zuk, 1982). In non-human vertebrates, studies have shown that secondary sexual characteristics may be reliable signals of immune function (see Moller et al., 1999 for a review). In the peacock *Pavo cristatus*, the barn swallow *Hirundo rustica*, the house sparrow *Passer domesticus*, and the lizard *Psammodromous algirus*,

the expression of secondary sexual characteristics are associated with measures of immune response: those individuals with more active immune systems have more extravagant displays than individuals with less active immune systems (Møller et al., 1999). Females may, therefore, choose males on the basis of their exaggerated secondary sexual characteristics in order to obtain heritable resistance to parasites and pathogens for their offspring, and males displaying reliable cues to this resistance are likely to have increased reproductive success.

Sexually dimorphic traits in humans develop during puberty. In males, the development of masculine traits is stimulated by a surge in testosterone (T), which causes increased growth of the jaw, brow ridge and cheekbones (Enlow, 1990). Masculinity in the face and body are therefore viewed as secondary sexual traits. Because of the immunosuppressive effects of T, large secondary sexual traits may signal genetic quality (Hamilton & Zuk, 1982; Wedekind, 1992) because males with genetic resistance to parasites and pathogens can afford the immunosuppression required to develop extreme masculine traits (Folstad & Karter, 1992). Thus, Folstad and Karter (1992) argued that a trade-off between the development of T-dependent traits and immunity makes secondary sexual traits honest signals of male health and vigour that females can utilise in mate choice. Females might therefore be expected to show a preference for masculine men, and by virtue of the link between T and the expression of masculinity, also men with high T levels.

Studies investigating the relationship between attractiveness and masculinity in humans have provided mixed results. Some find that masculine faces or masculine body traits such as height, shoulder width and muscularity are attractive (Cunningham et al., 1990; Barber, 1995), while others find a female preference for feminised facial features (Perrett et al., 1998; Penton-Voak et al., 1999). These mixed findings may represent a trade-off that females must face in choosing a mate. Although masculine traits may signal mate quality, females rate men with feminised faces as more cooperative and honest, and less dominant (Perrett et al., 1998) which may make less masculine males more preferred as a long term mate. Females may be prepared to risk mating only with a masculine male, with associated negative costs such as aggression and dishonesty, when that copulation may result in a pregnancy thus gaining genetic benefits for offspring. Indeed, several studies have shown an increase in preferences for masculinity when the chance of conception is high (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Little et al., 2007). These cyclic shifts are

argued to be an adaptation for obtaining a high-quality mate during the cycle phase when intercourse is most likely to result in a pregnancy (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000). However, cyclic shifts in visual preferences have been shown only in studies that require female choices to be made between subtle variants of the same computer-generated identity. This evidence would be much stronger, and more applicable to actual human mate choice if the same effect could be shown using natural stimuli, in a biologically relevant context.

### **1.2 MATE QUALITY MAY ALSO BE SIGNALLED BY SYMMETRY AND AVERAGENESS.**

Two other traits that are preferred in potential mates because they may honestly signal mate quality, are bilateral symmetry and averageness (where traits conform to a population average configuration) (Thornhill & Gangestad, 1999; Rhodes, 2006). Symmetry and averageness may reflect an individual's ability to cope with environmental and genetic stresses throughout development (Møller & Swaddle, 1997; Thornhill & Møller, 1997; Fink & Penton-Voak, 2002). Symmetry in bilaterally paired traits is thought to signal the ability to withstand the harmful effects of developmental perturbations caused by toxins and pathogens and genetic abnormalities. Individuals who are unable to resist the harmful effects of developmental perturbations caused by toxins and pathogens are likely to exhibit more asymmetries and less average (i.e. more distinctive) features. Indeed in non-human animals body asymmetry reflects increased inbreeding, parasite load, and poor condition (Parsons, 1990; Møller & Swaddle, 1997; Polak, 2003), while in humans, measurements of body asymmetry indicates general (ill) health, inbreeding (Livshits & Kobylansky, 1991; Thornhill & Møller, 1997) and lower semen quality (Manning et al., 1998; Firman et al., 2003). Moreover, because secondary sexual traits are typically costly to produce, they may be especially sensitive to developmental instability during their development, and particularly revealing of a male's genetic quality (Møller, 1993). Therefore, females might be expected to pay particular attention to symmetry and averageness of secondary sexual traits during mate choice.

### **1.3 MEASURES OF MATE QUALITY.**

Human mate preferences for sexual dimorphism, symmetry and averageness translate to greater mating success for those individuals who possess high levels of each trait (Rhodes et al., 2005). Although it is hypothesised that attractive traits signal mate

quality, and mate preferences have been studied extensively (Rhodes, 2006), studies of the direct links between visual preferences and specific aspects of mate quality have been less prolific.

Two male traits that could be used as a measure of mate quality are semen quality, because it represents reproductive potential (Bonde et al., 1998) and T level, because of its interplay with immunity and disease. Testosterone might also reflect mate quality because its immunosuppressive effects may favour spermatogenesis. Sperm cells are perceived as non-self by the immune system, and are exposed to immunological attack by the immune system (Skau & Folstad, 2005). Therefore local immunosuppression by androgens like T is important for reducing immunological responses against sperm cells. Indeed low fertility may be due to an inability to conduct immunosuppression (Folstad & Skarstein, 1997; Skau & Folstad, 2003). If the development of male secondary sexual characteristics is associated with immunosuppression conducted by T (Folstad & Karter, 1992; Folstad & Skarstein, 1997), then secondary sexual characteristics could therefore provide females with reliable information not only about resistance to infectious diseases, but also semen quality.

A female preference for males with high levels of these traits would increase her reproductive success via indirect benefits associated with 'good genes' and increased offspring fitness. Furthermore, a female could gain direct benefits by mating with a male who is relatively parasite and disease free thereby decreasing her own risk of illness, or who has high fertility, thereby increasing her chances of conception. It is unclear, however, whether females are sensitive to visual cues to current T levels or semen quality in the male face and body, whether they are preferred and, if a preference exists, whether the preference changes according to the probability of conception throughout the menstrual cycle.

#### **1.4 THESIS APPROACH AND AIMS.**

Studies that have investigated the importance of visual preferences and aspects of mate quality in human mate choice have tended to concentrate on facial features, while body appearance has been largely ignored. In contrast, similar studies of secondary sexual characteristics and symmetry in non-human animals have generally focussed on body traits. This thesis will aim to bring this study of humans into line with the animal literature, by including both faces and bodies in all of the studies herein.

This thesis will address the broad hypothesis that testosterone-linked masculine traits in the face and body signal mate quality, and that females are sensitive to these cues. In order to more fully understand the mechanisms behind sexual selection acting on males, a series of four studies will investigate the inter-relationships between masculinity, symmetry and/or averageness of face and body, and mating success, T, and semen quality, using one large male sample. The first study will investigate the relative contributions of the face and the body when opposite sex attractiveness judgements are made. The second study will examine whether female preferences for masculine and symmetric faces and bodies change through the menstrual cycle by using real photographs of men, to attempt to generalise previous findings to a biologically relevant context. The third study will investigate whether a mate choice preference exists for males with high T, by studying the interrelationships between appearance (including attractiveness and masculinity), testosterone and sexual behaviour. The final study will investigate whether masculinity, symmetry and averageness are honest signals of mate quality, by investigating whether each of these traits provide information about the reproductive potential of a male.

Together, these studies will test the hypothesis that faces and bodies signal honest information about mate quality, in terms of T levels and semen quality, and that female preferences are adaptations for finding good quality mates. The specific aims are:

- To determine whether faces and bodies each provide cues that may be associated with mate quality and important to human mate choice (Chapter 2)
- To examine whether prior evidence for increased preferences for masculinity and symmetry at the fertile point of the menstrual cycle generalise to a biologically relevant context by using real photographs of men (Chapter 3) and whether cyclic preference shifts reflect increased preferences for a superior quality mate (Chapter 5).
- To investigate whether secondary sexual traits honestly signal T levels, and whether females show a preference for males with high T (Chapter 4).
- To investigate the extent to which masculinity, symmetry and averageness are honest signals of semen quality, and whether females show a preference for men with high semen quality (Chapter 5).

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## **CHAPTER TWO**

# **CONTRIBUTIONS OF THE FACE AND BODY TO OVERALL ATTRACTIVENESS.**

## **CHAPTER TWO: CONTRIBUTIONS OF THE FACE AND BODY TO OVERALL ATTRACTIVENESS.**

### **2.1 ABSTRACT.**

Faces and bodies are thought to be signals of mate quality in humans. Most research on attractiveness has focused on faces or bodies separately, while our preferences have evolved based on both seen together. A fundamental requirement of studying face and body attractiveness independently is that there is no interaction between the two. This study is the first to investigate whether the interaction between rated attractiveness of the face and the body predicted ratings of overall attractiveness. We found that the face and body did not interact when an overall attractiveness judgment is made. We also investigated the independent contributions of rated attractiveness of the face and the body to ratings of overall attractiveness. Face and body attractiveness each made significant independent contributions to overall attractiveness in males and females. For both sexes, facial attractiveness predicted overall attractiveness more strongly than did body attractiveness, and this difference was significant in males. The contributions of components of face and body attractiveness (symmetry, sexual dimorphism and averageness) to overall attractiveness were also examined using principal components analysis. A component associated with attractive traits in the male face, and in females both a face and body component, significantly predicted overall attractiveness. Our results validate the assumption that studying faces and bodies separately in the context of mate choice will produce biologically meaningful results and suggest that face and body attractiveness may convey potentially independent signals about an individual's mate quality.

## 2.2 INTRODUCTION.

Human perceptions of attractiveness have been studied extensively, particularly in the context of mate choice (Thornhill & Gangestad, 1999; Zebrowitz & Rhodes, 2002; Grammer et al., 2003). Attractiveness enhances mating success in humans, suggesting that both attractive traits and preferences for those traits may be sexually selected (Rhodes et al., 2005). Evolutionary psychologists argue that perceptions of attractiveness are adaptations for finding a good quality mate (see Thornhill & Gangestad, 1999; Rhodes, 2006 for reviews), either because they identify high quality individuals or because benefits can be gained by associating with attractive people because they are treated more favourably (the "beauty is good" stereotype - Dion et al., 1972) (Udry & Eckland, 1984; Kalick et al., 1998). Alternatively, it has also been argued that perceptions of attractiveness evolved as a by-product of information processing mechanisms (e.g. recognition or perception) in the brain (Enquist et al., 2002). It is also possible that these accounts are not mutually exclusive, and that both kinds of selection pressure may have shaped human preferences.

Perceptions of attractiveness have certainly evolved in the context of faces and bodies seen together, yet almost all of the research on attractiveness has investigated facial or body attractiveness separately. This gives rise to two major issues that have not been addressed thus far: First, whether there is an interaction between faces and bodies, and second what contribution each makes to overall attractiveness. If there is an interaction between face and body attractiveness, then faces and bodies cannot meaningfully be studied separately and mate-choice studies based solely on facial or body attractiveness are fundamentally flawed. If there is no interaction, and the face and the body each make independent contributions to overall attractiveness, then attractiveness studies based on only one of these components are valid, but more information could be gained from studying both. The size of each independent contribution is important. If, for example, one makes a large contribution to overall attractiveness, while the other contribution is very small, then this larger contributor may be a better focus for future mate choice studies.

Little is known about the relationship of face and body attractiveness to overall attractiveness (Henss, 2000). Nothing is known about this relationship in males and only two studies have examined the relationship in females, both of which are weak methodologically (Mueser et al., 1984; Alicke et al., 1986). Mueser et al. (1984) used a small number of photographed individuals (hereafter referred to as "models") and very

few raters. They found that facial attractiveness accounted for 28% of the total variance of overall female attractiveness, and body attractiveness accounted for 20% of the variance. However, these contributions to overall attractiveness may have been underestimated due to limited range because analyses were conducted using only 15 female models and seven male raters per group (face, body, or overall attractiveness). Alicke et al. (1986) used computer-manipulated images, mixing and matching faces and bodies, so the natural associations could not be examined. They combined three levels (low, medium and high) of facial and body attractiveness, and had the resulting 27 images rated for attractiveness by males and females. Overall attractiveness ratings increased as facial attractiveness and body attractiveness increased. While not specifically measuring the contributions of the face and the body to overall attractiveness, Alicke et al. (1986) found overall attractiveness ratings were reduced considerably more when a high-attractive face was combined with a low-attractive body, compared with a low-attractive face/high-attractive body combination. This suggests that the body might be more important than the face as a component of overall attractiveness.

Here, we aim to determine whether there is an interaction between face and body attractiveness when overall attractiveness judgments are made. In order to continue studying faces and bodies separately in the context of mate choice there must be no interaction between these two components. We also aim to quantify the contributions of the face and the body to judgments of overall attractiveness of both females and males. We extend previous research by using unmanipulated photographs to avoid anomalies that may arise from mixing up heads and bodies (Alicke et al., 1986), and using large samples of both models and raters.

Several traits have been widely associated with attractiveness in humans, most notably symmetry, averageness and sexual dimorphism (masculinity in males, femininity in females) (for a review, see Rhodes, 2006). Ratings of symmetry, averageness and sexual dimorphism are significantly correlated with measurements of those same traits in faces (Rhodes & Tremewan, 1996; Koehler et al., 2004; Simmons et al., 2004). Thus, ratings reflect the actual degree to which each trait is present, at least in faces. We also investigated which attractive face and body traits drive overall attractiveness judgments, by examining the associations of these attractive traits with overall attractiveness.

## **2.3 METHOD.**

### **2.3.1 RATERS.**

Twenty-four (12 male, 12 female) Caucasian students at the University of Western Australia participated, following informed consent, in return for course credit or remuneration of travel costs. Male and female raters were aged 18 - 25 years ( $X \pm SD = 20.1 \pm 2.6$  years,  $N = 12$ ) and 17 - 27 years ( $X \pm SD = 18.9 \pm 2.8$  years,  $N = 12$ ) respectively.

### **2.3.2 STIMULI.**

Coloured, front-view face, body (no-head), and full-length (head and body) digital photographs were obtained from the Facelab Database (School of Psychology, University of Western Australia) (see Rhodes et al., 2005 for details) ( $n$  (females)=80;  $n$  (males)=84). Photographs were taken under symmetric lighting conditions from a fixed distance of 190cm. In these photographs, posers wore shorts and a t-shirt, stood with arms relaxed at their sides and adopted a neutral facial expression. Full-length and body images were presented at 450 pixels in height (width varying). Faces were presented surrounded by a black oval mask (outer dimensions 320x420 pixels) that covered most of the hair. All images were presented at a resolution of 72 pixels per inch.

### **2.3.3 PROCEDURE.**

Participants were asked to rate opposite sex, full-length photographs for overall attractiveness on a seven-point Likert scale (1 = not attractive at all; 7 = very attractive). The photographs were presented in random order on a computer screen and remained visible until a response was given. Ratings of recognized individuals were removed from the dataset. Inter-rater reliability was high with Cronbach alphas of 0.85 and 0.92 for male and female raters respectively. A mean overall attractiveness rating was calculated for each individual by averaging the ratings given by each of the 12 opposite-sex raters (female models: Mean=3.1, SD=0.8; male models: Mean=3.1, SD=1.0).

Separate face and body ratings of attractiveness, masculinity/femininity, symmetry and averageness were taken from Rhodes et al. (2005).

## **2.4 RESULTS.**

Descriptive statistics for ratings of face and body attractiveness, averageness, symmetry, and masculinity/femininity are shown in Table 1.

A preliminary analysis of Pearson correlations between all variables is shown in Appendix 1. While numerous significant correlations were found, the following is a

summary of those that are central to this study. For males, face and body attractiveness were significantly correlated with overall attractiveness but not with each other. Face and body sexual dimorphism (masculinity) were significantly correlated with each other, and face sexual dimorphism was also significantly correlated with overall male attractiveness. Facial symmetry, sexual dimorphism and averageness in males were significantly correlated with facial attractiveness. Male body attractiveness was significantly correlated with body averageness and body sexual dimorphism, but not body symmetry.

For females, face and body attractiveness were significantly correlated with each other and with overall attractiveness. Female facial attractiveness was significantly correlated with facial symmetry, averageness and sexual dimorphism (femininity). Female body attractiveness was significantly correlated with face and body sexual dimorphism, but not with body symmetry or averageness. Significant correlations were also found between overall female attractiveness and face and body sexual dimorphism.

To determine the relative contributions of the face and body to overall attractiveness, separate multiple regression analyses were conducted for males and females with ratings of overall attractiveness as the dependent variable and ratings of face and body attractiveness and an interaction term (face attractiveness x body attractiveness) as the independent variables (Table 2). Both regression models were highly significant, accounting for 35.3% ( $F_{(3,80)}=14.53$ ,  $p<0.0001$ ) and 41.8% ( $F_{(3,76)}=18.22$ ,  $p<0.0001$ ) of the variance in male and female overall attractiveness respectively. Face and body attractiveness were both significant predictors of overall attractiveness in males and females. The interaction between face and body attractiveness did not predict overall attractiveness in either model (Table 2). Facial attractiveness was a numerically stronger predictor than body attractiveness in both sexes. Standardised Betas for face and body attractiveness were compared using Cohen and Cohen's (1983) test for difference between two independent correlation coefficients, which converts each coefficient to a z-score and compares these values. Facial attractiveness was a significantly stronger predictor of overall attractiveness than body attractiveness in males, but not in females ( $Z \text{ Diff}_{\text{males}} = 2.12$ ,  $p=0.033$ ;  $Z \text{ Diff}_{\text{females}} = 1.08$ ,  $p=0.281$ ).

We also wanted to assess the contribution of the various rated components of face and body attractiveness to overall attractiveness. Multiple regression analyses can be limited by multicollinearity between the predictor variables (see Appendix 1). We

therefore conducted a principal components analysis (PCA) to derive a set of independent predictor variables. Separate PCAs for males and females were conducted. We found two factors that captured face and body attractiveness respectively. Together they accounted for 49.9% (males) and 49.4% (females) of the total variance in the variables (Table 3). The first principal component (PC1) in the male PCA was a body attractiveness factor that loaded significantly on body attractiveness, body sexual dimorphism and body averageness. It accounted for 29.7% of the variation. The second principal component (PC2) in the male PCA was primarily associated with attractive face traits and loaded significantly on face attractiveness and face sexual dimorphism. PC2 represented 20.2% of the sample variance. Conversely in the female PCA, PC1 was primarily associated with face traits (face attractiveness, symmetry and sexual dimorphism) and accounted for 30.4% of the variance while PC2, accounting for 19.0% of the variance, was associated mainly with body traits (body attractiveness, symmetry, sexual dimorphism and averageness), as well as one face trait (face averageness).

These two components, along with an interaction variable (PC1 x PC2), were entered as predictors of overall attractiveness in multiple regression analyses for males and females separately. These variables combined to account for 32.2% of the variance in male overall attractiveness ( $F_{(3,80)}=12.6, p<0.0001$ ) and 38.0% of the variance in female overall attractiveness ( $F_{(3,76)}=15.5, p<0.0001$ ). The “face” component, PC2, was the only significant predictor of overall attractiveness in males. Both the “face” and “body” components significantly predicted female overall attractiveness (Table 4). The interaction component did not significantly predict overall attractiveness in either males or females.

## **2.5 DISCUSSION.**

Attractiveness is important in human mate choice. However, most studies have investigated facial attractiveness and body attractiveness separately, while our preferences have evolved based on the whole (face and body together). This study showed that rated face and body attractiveness contribute independently and substantially, with no interaction, to overall female and male attractiveness. For females in our study, rated face attractiveness and rated body attractiveness accounted for 47% and 32% of the variance in overall attractiveness. These are higher than the values of 28% and 20% respectively, obtained by Mueser et al. (1984) with a very small sample of models, consistent with our suggestion that their low sample size may have lead to

underestimates of these contributions in their study. For males, rated face and body attractiveness respectively accounted for 52% and 24% of the variance in overall attractiveness. Our study is the first to measure the independent contributions of the face and body to overall male attractiveness. Importantly, face and body attractiveness did not significantly interact in predicting overall attractiveness in males or females. These results are critical because they confirm and quantify the assumption that the face and body both contain independent cues to overall attractiveness. Thus, even though our preferences have evolved by viewing the whole person, overall attractiveness judgments are based on separate, unique contributions of the face and body, with no interaction between the two. Previous studies have generally studied faces and bodies separately. For example, Rhodes et al. (2005) showed that face and body attractiveness (separately) are each associated with sexual behaviour. This study gives evidence that results such as these, are biologically relevant: No interaction between face and body attractiveness means that each can be meaningfully studied independently of the other.

Surprisingly, the variance in overall attractiveness explained by the sum of rated face attractiveness and rated body attractiveness was modest (35-42%). We established that the unexplained variance was not due to an interaction between predictors. Some of the unexplained variance may be due to differences in the presentation of the photographs. There was a notable size difference in the presentation of the face stimuli depending on whether they were presented separately or together (as a whole) i.e. the faces were much larger when presented alone on the screen compared to when presented as part of a whole. This allowed a more detailed assessment to be made of the face-only image, compared with whole image. Additionally, face photos were masked, with hair cues removed, whereas the whole body (head included) photos were shown with hair. It is also possible that the whole images are processed holistically, and so are more than the simply the sum of two parts (Reed et al., 2003).

It has been proposed that attractiveness preferences have evolved to facilitate the detection of a high quality mate, favouring healthy, parasite-resistant individuals (Thornhill & Gangestad, 1993). Thus, physical attractiveness is thought to be an honest indicator of genotypic and phenotypic quality. If this is true, then our results confirm the often-held assumption that the face and the body both contain cues to mate quality in both males and females. Interestingly, the rated attractiveness of the face was a stronger predictor of overall attractiveness than was rated attractiveness of the body and this difference was significant for male attractiveness. This may partly be because the face is

simply more salient than the body because of its important role in human social interactions, given its display of facial expressions of emotion, eye gaze cues to the direction of attention and lip movements associated with speech. This may be particularly relevant for women who are better than men at both expressing emotion (Palermo & Coltheart, 2004) and recognizing facial expressions (Hall, 1978). This finding might also be partly attributed to the fact that the bodies were clothed and the faces unadorned. If we had presented naked bodies it is possible the body contribution would have increased, consistent with Alicke et al.'s (1986) suggestion that bodies were more important than faces after presenting faces with bodies in bathing suits. However, studies of mate-choice are as much about current behaviour as they are about that of our early human ancestors. It is therefore more relevant to present clothed bodies in an experimental setting because it more accurately reflects how bodies are viewed when making present-day mate-choice decisions.

Thornhill and Grammer (1999) reported a moderate association (0.30) between face and body attractiveness for a sample of female models who volunteered to pose naked. Our results extend this result to a (clothed) female student sample ( $r = 0.326$ ), but not to a male student sample ( $r = 0.134$ ). Thornhill and Grammer (1999) interpreted the association between face and body attractiveness as evidence that the face and body form a single condition-dependent ornament, arguing that face and body attractiveness would not be associated if they did not reflect condition. However, we suggest that a moderate association could arise from individual differences that are unrelated to condition, such as differences in grooming. Our results also suggest that face and body attractiveness are not a single ornament. If they are, then they should have loaded on the same factor in a principal components analysis, but they did not. Instead relatively distinct “face” and “body” attractiveness components emerged from the PCA for both female and male attractiveness. Further evidence that the face and body do not form a single ornament comes from our findings that a large amount of the variance in face and body attractiveness remains unshared and that rated attractiveness of each makes independent contributions to overall attractiveness. We speculate that bodies and faces may reflect different aspects of mate quality. The body may be more responsive to lifestyle choices, such as exercise, fashion and grooming. Face structure, however may be a more stable and honest indicator of heritable aspects of mate quality.

Symmetry, averageness and sexual dimorphism (masculinity/femininity), have each been associated with attractiveness in the face and/or body (see Rhodes, 2006 for a

review) but their roles in overall attractiveness judgments have not been investigated prior to this study. Principal components analyses of attractive traits in the face and body yielded distinct “body” and “face” attractiveness components. For males, only the “face” component (associated with facial attractiveness and sexual dimorphism) significantly predicted overall attractiveness suggesting that significantly more cues were drawn from the face than from the body (specifically from masculine facial features), when a full-length male photo (face/head and body visible) was presented to females. The expression of masculine facial traits (secondary sexual characteristics) may reflect an effective immune system and resistance to diseases or parasites because hormones that are responsible for the development of these traits may compete with the immune system (Hamilton & Zuk, 1982; Folstad & Karter, 1992; Gangestad & Buss, 1993; Rhodes et al., 2003). The male “body” component (comprising body attractiveness, sexual dimorphism and averageness) did not predict overall attractiveness. In contrast rated face and body attractiveness both predicted overall male attractiveness, although face attractiveness was the stronger predictor. The use of independent face and body components, obtained by PCA, appears to have amplified this difference in contribution of the face and body to overall male attractiveness. There may also be other attractive body trait(s), not assessed in these analyses, which explain the contribution of rated body attractiveness to overall male attractiveness. A more specific measurement like shoulder-to-hip ratio may have been a useful inclusion. Shoulder-to-hip ratio, in males, is associated directly with androgen levels and significantly associated with sexual behaviours (Hughes & Gallup, 2003) suggesting that women may use SHR in their assessment of partner choice.

For females, the “face” component was associated with face attractiveness, symmetry and sexual dimorphism, and the “body” component was associated with body attractiveness, symmetry, sexual dimorphism and averageness. The body component was also associated with face averageness. Both components were significant predictors of overall attractiveness and the interaction term was not a significant predictor. Therefore, all of the attractive traits used as variables in the female PCA (captured either by PC1 or PC2) were used by male raters when making overall female attractiveness judgments. Symmetry, sexual dimorphism and averageness each reflect developmental stability, immuno-handicaps and prototypical configuration respectively (Grammer et al., 2003) and could give males information about a female’s genotypic

and phenotypic quality, and reproductive capability (Grammer et al., 2003; Rhodes, 2006).

This study is the first to show that the interaction between face and body attractiveness does not predict overall attractiveness. This was true both for rated face and body attractiveness and for independent components of face and body attractiveness obtained using principal components analysis. Furthermore, we have shown that rated face and body attractiveness both make independent contributions to overall attractiveness. These results are important because they substantiate the often-held assumption that studying faces and bodies separately in the context of mate choice is a valid approach. To the extent that perceptions of attractiveness influence mate choice, it is overall attractiveness that drives choices. Mate choice studies that are based on only face or body attractiveness will yield biologically significant results, but would be improved by including both elements.

## **2.6 ACKNOWLEDGEMENTS.**

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Table 1. Average values ( $\pm$  SE) for attractiveness variables. Ratings are opposite sex ratings ie. Ratings of males made by females and ratings of females made by males.

Attractiveness Variable	Males (n=84)	Females (n=80)
Overall attractiveness	3.1 ( $\pm$ 0.1)	3.1( $\pm$ 0.4)
Face attractiveness	3.0 ( $\pm$ 0.1)	3.2 ( $\pm$ 0.1)
Face symmetry	3.9 ( $\pm$ 0.1)	4.3 ( $\pm$ 0.1)
Face sexual dimorphism <sup>1</sup>	4.3 ( $\pm$ 0.1)	3.9 ( $\pm$ 0.1)
Face averageness	3.3 ( $\pm$ 0.1)	3.2 ( $\pm$ 0.1)
Body attractiveness	3.4 ( $\pm$ 0.1)	3.6 ( $\pm$ 0.1)
Body symmetry	4.3 ( $\pm$ 0.1)	4.6 ( $\pm$ 0.1)
Body sexual dimorphism <sup>1</sup>	4.2 ( $\pm$ 0.1)	4.1 ( $\pm$ 0.1)
Body averageness	3.5 ( $\pm$ 0.1)	3.3 ( $\pm$ 0.1)

<sup>1</sup>masculinity in males, femininity in females

Table 2. Multiple regression models: Face and body attractiveness as predictors of overall attractiveness.

Predictor variable	Male attractiveness (d.f.=81)				Female attractiveness (d.f.=77)			
	B ( $\pm$ SE)	$\beta$	<i>t</i>	<i>P</i>	B ( $\pm$ SE)	$\beta$	<i>t</i>	<i>P</i>
Face attractiveness	0.61 (0.11)	0.517	5.67	<0.0001*	0.37 (0.08)	0.468	4.89	<0.0001*
Body attractiveness	0.29 (0.11)	0.235	2.58	0.012*	0.35 (0.10)	0.322	3.42	0.001*
Face*Body attractiveness <sup>§</sup>	0.08 (0.12)	0.055	0.61	0.542	-0.03 (0.10)	-0.030	-0.32	0.747

<sup>§</sup> Variables are centered around their means for interaction terms. Male interaction term: (Face attractiveness - 3.034) \* (Body attractiveness - 3.429); Female interaction term: (Face attractiveness - 3.159) \* (Body attractiveness - 3.642).

Table 3. Principal components analysis of attractive traits in the face and body for males and females.

	Component (Males)		Component (Females)	
	1	2	1	2
Face attractiveness	-0.087	0.856*	0.901*	0.005
Face symmetry	0.167	0.471	0.641*	-0.044
Face sexual dimorphism <sup>1</sup>	-0.037	0.795*	0.895*	0.084
Face averageness	0.147	0.371	0.351	0.602*
Body attractiveness	0.835*	0.216	0.477	0.570*
Body symmetry	0.131	0.297	0.085	0.420*
Body sexual dimorphism <sup>1</sup>	0.790*	0.204	0.123	0.551*
Body averageness	0.827*	0.048	0.142	0.602*

For each component, variables that had loadings greater than 70% of the largest loading were considered to be significant contributors to that component (Mardia et al., 1979) (indicated by \*).

Table 4. Multiple regression models: Attractive traits in the face and body as predictors of overall attractiveness.

Predictor variable	Male attractiveness (d.f. = 76)				Female attractiveness (d.f. = 71)			
	B ( $\pm$ SE)	$\beta$	<i>t</i>	<i>P</i>	B ( $\pm$ SE)	$\beta$	<i>t</i>	<i>P</i>
“Face” Component	0.58 (0.10)	0.56	6.07	<0.0001*	0.44 (0.07)	0.56	6.02	<0.0001*
“Body” Component	0.10 (0.10)	0.10	1.06	0.293	0.14 (0.07)	0.18	2.02	0.047*
“Face” Component x “Body” Component	-0.06 (0.09)	-0.06	-0.61	0.541	0.06 (0.07)	0.08	0.89	0.376

For males the “face” component is PC2 and the “body” component is PC1. For females the “face” component is PC1 and the “body” component is PC2

Appendix 1. Zero order correlations between all variables. N=84 (males), 80 (females). Correlations for males (rated by females) are above the diagonal, and correlations for females (rated by males) are below.

	Overall attractiveness	Face attractiveness	Face symmetry	Face sexual dimorphism <sup>1</sup>	Face averageness	Body attractiveness	Body symmetry	Body sexual dimorphism <sup>1</sup>	Body averageness
Overall attractiveness	1	0.544***	0.102	0.457***	0.203	0.304**	0.113	0.211	-0.008
Face attractiveness	0.567***	1	0.247*	0.549***	0.277*	0.134	0.155	0.055	-0.018
Face symmetry	0.192	0.464***	1	0.179	0.155	0.168	0.040	0.165	0.102
Face sexual dimorphism <sup>1</sup>	0.534***	0.828***	0.443***	1	0.056	0.149	0.143	0.254*	-0.097
Face averageness	0.177	0.224*	0.066	0.174	1	0.100	0.026	0.072	0.184
Body attractiveness	0.478***	0.326**	0.146	0.339**	0.034	1	0.182	0.619***	0.537***
Body symmetry	0.052	0.076	0.136	0.049	-0.119	0.116	1	0.041	0.093
Body sexual dimorphism <sup>1</sup>	0.225*	-0.022	-0.141	0.152	-0.032	0.499***	-0.052	1	0.464***
Body averageness	-0.012	-0.0004	0.004	0.026	0.341**	-0.003	-0.215	-0.021	1

<sup>1</sup>Masculinity in males, femininity in females

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

## **CHAPTER THREE**

**PHOTOGRAPHS OF MALE FACES AND BODIES PROVIDE  
NO EVIDENCE FOR A PREFERENCE SHIFT FOR  
MASCULINITY OR SYMMETRY ACROSS THE MENSTRUAL  
CYCLE.**

# **CHAPTER THREE: PHOTOGRAPHS OF MALE FACES AND BODIES PROVIDE NO EVIDENCE FOR A PREFERENCE SHIFT FOR MASCULINITY OR SYMMETRY ACROSS THE MENSTRUAL CYCLE.**

## **3.1 ABSTRACT.**

Previous studies have shown that women increase their preference for masculinity, during the fertile phase of the menstrual cycle. Evidence for a similar preference shift for symmetry is equivocal. Previously, studies have required participants to choose between subtle variations in computer-generated stimuli, which may not capture functional female responses that influence mate-choice. Our study employed photographs of individual males to investigate preferences for face and body masculinity and symmetry during the menstrual cycle. We collected attractiveness ratings from 25 normally cycling women at high and low fertile days of the menstrual cycle. Attractiveness ratings were correlated with masculinity and symmetry ratings provided by independent sets of raters. We found no evidence for any cyclic shift in female preferences. There was no significant difference between high and low fertility ratings of attractiveness. Furthermore, correlations between attractiveness and masculinity, and attractiveness and symmetry did not differ significantly between high and low fertility. These results suggest that a menstrual cycle shift in visual preferences may be too subtle to influence responses to real faces and bodies, and raise doubts about the biological relevance of previous findings.

### 3.2 INTRODUCTION.

Mate preferences, and indeed mating behaviour, are strongly influenced by morphological traits exhibited by a potential partner (Barber, 1995; Rhodes et al., 2005). Potential mates must be assessed based on the costs and benefits associated with traits they display. Both masculinity and symmetry are traits that enhance physical attractiveness in humans (Rhodes, 2006), potentially because they are honest signals of male genetic quality (Gangestad & Thornhill, 1997). Masculinity may signal immunocompetence and parasite load because testosterone, which triggers the development of masculine traits during adolescence, is an immunosuppressant and only individuals in good condition can afford exaggerated secondary sexual traits (Hamilton & Zuk, 1982; Folstad & Karter, 1992). Symmetry is also thought to indicate genetic quality. Bilateral symmetry is the developmental norm, and random deviations from symmetry are thought to reflect perturbations to normal development arising from a life-history of general (ill) health (for reviews see Moller & Swaddle, 1997; Polak, 2003). Individuals of lower genetic quality are more likely to have disrupted developmental stability, and this is argued to be reflected in an increase in asymmetry. Therefore, a preference for masculine and/or symmetric traits could allow women to obtain mates in good condition, which might confer disease-resistance and other genetic benefits to their offspring.

There is evidence that women's preferences are not stable, but rather appear to exhibit an adaptive shift that co-varies with the chance of conception, whereby preferences are stronger during the fertile window of the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000). Several studies have shown an increase in women's visual preferences for relatively more masculine faces (e. g. Frost, 1994; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001), bodies (Pawlowski & Jasienska, 2005; Little et al., 2007a), and voices (Puts, 2005; Feinberg et al., 2006) during the fertile phase of the menstrual cycle. Furthermore, in a study of olfactory preferences, Havlicek, Roberts and Flegr (2005) found a positive correlation between questionnaire-assessed male dominance, and females perceptions of male odour 'sexiness' at their fertile point of the menstrual cycle, but not in other cycle phases.

This cyclic effect on visual masculinity preferences seems to be influenced by relationship context. Penton-Voak et al. (1999) studied both short-term and long-term

partner preferences, and found that women showed a cyclic shift in preference for masculinity only when selecting for a short-term partner.

This increased preference when the chance of conception is high is argued to maximise potential genetic benefits that a masculine male might provide, while concurrently minimising associated costs. Masculinity has been associated with dominance and reduced parental care, and females must trade-off genetic benefits against parental investment (e.g. Perrett et al., 1998). This trade-off is supported by evidence that cyclic shifts are present only when selecting for a short-term, but not long-term partner (Penton-Voak et al., 1999). A complementary hypothesis used to explain cyclic shifts in masculinity preferences argues for a central role for the hormone progesterone, the hormone that is present in elevated concentrations during pregnancy, and during the luteal phase (after ovulation and before the onset of menses) (Jones et al., 2005). This argument proposes that an increased preference for less masculine men and an increase in relationship commitment during the luteal phase, reflects an adaptive strategy that may minimise costs and provide increased paternal investment during times when the hormone profile mimics pregnancy (Jones et al., 2005a). The benefits of a cyclic shift in preferences may be two-fold: maximising preferences for good genes to pass on to offspring (indirect benefits) when conception is likely, and increasing preferences for traits that signal parental investment (direct benefits) on days that reflect the hormone profile of pregnancy, and correspond with a low chance of conception.

A preference for symmetry in a potential mate might also maximise heritable fitness benefits. Although symmetry is found to be generally attractive (see Rhodes, 2006, for a review), evidence for an increase in visual symmetry preferences at high fertility is weaker than that for masculinity preferences. Several studies have shown an increase in female olfactory preference for males with low levels of asymmetry, whereby the odour of symmetrical men was rated as more attractive during high fertility days of the menstrual cycle (i.e., during ovulation) (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999b; Thornhill et al., 2003). However, there is only one study that has found evidence for an increase in visual preferences for facial symmetry (Little et al., 2007b). In contrast, three separate studies found no evidence of an enhanced visual preference for facial symmetry during the ovulatory phase (Koehler et al., 2002; Cardenas & Harris, 2007; Oinonen & Mazmanian, 2007). There are no published studies that have investigated visual preferences for body symmetry over the menstrual cycle. Because body symmetry may

be an indicator of general health (Thornhill & Møller, 1997), it may also be a good candidate for a preference that would be amplified at the fertile point.

Prior menstrual cycle studies of visual preferences have potential methodological limitations. First, they may lack real-world validity. In contrast with olfactory studies that are based on real odours of actual men (generally the stimuli are t-shirts worn by males for a length of time), studies of menstrual cycle shifts in visual preferences have relied on the use of computer-generated faces that are manipulated to reflect different levels of symmetry or masculinity. All three studies of facial masculinity preferences used computer-generated composite stimuli, constructed by morphing several faces together, and then “masculinising” or “feminising” them (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001). This manipulation involves exaggerating or reducing features according to differences between an average male and average female, for example as male jaws are larger than female jaws, a “masculinised” male face will have a larger jaw than the average male. Little et al.’s (2007a) study of masculinity in male bodies also used similar computer graphics techniques to construct masculinised and feminised versions of the same body. Likewise, the studies of cyclic shifts in visual preferences for symmetry also presented faces that were computer-altered to illustrate varying levels of symmetry (see Koehler et al., 2002; Cardenas & Harris, 2007; Little et al., 2007b; Oinonen & Mazmanian, 2007). In all cases, female participants responded to different variations of the same male identity, either by choosing between a high and low trait version of the same face, or by selecting a preferred version of a face from a continuum. While this methodology may provide a very sensitive measure of women’s perceptions, it may lack biological relevance if the small changes in women’s preferences observed using these artificial stimuli do not translate to real world mate choice decisions.

Faces and bodies in the real world do not vary on only one continuum or trait, nor do women choose their mates based on variations within the same individual. In reality, women choose their mates based on faces and bodies that vary simultaneously on many traits. When actual behaviours are being interpreted from preferences, it is important to demonstrate that the effect is not detectable only in computer-generated faces because the preferences they elicit may not be a true reflection of decisions that are made in the mate-choice process.

No studies have shown any direct links between likelihood of conception and preferences for morphological traits using images of real people. Attractiveness,

symmetry and masculinity ratings of male face and body photographs are significantly correlated with the photographed individual's mating success (Rhodes et al., 2005; Peters et al., 2008). Unmanipulated photographs therefore contain biologically relevant information that may direct actual female choice. The evidence for a menstrual cycle shift in preferences would be stronger if the effects that are found using artificial stimuli can also be shown using photographs of real men.

A second methodological issue concerning menstrual cycle studies is the classification of the "fertile window". Previously, most studies have relied on self-reported menstrual-cycle data and classified a wide range of cycle days as "fertile" (see for example Gangestad & Thornhill, 1998; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Koehler et al., 2002; Havlicek et al., 2005; Pawlowski & Jasienska, 2005; Cardenas & Harris, 2007; Little et al., 2007a; Little et al., 2007b). Self-reported cycle lengths are prone to high measurement error, with 43% of women mis-reporting cycle length by 2 or more days in a study by Small, Matunga and Marcus (2007). Additionally, using self-reported menstrual cycle data to estimate ovulation assumes that the luteal phase consistently begins 14 days prior to the onset of the next menses. However the luteal phase can vary between 4 and 19 days in length (Stern & McClintock, 1998). These self-reported menstrual cycle data therefore allows misclassification and underestimation of any cyclic effects (although they do appear to provide accurate enough information to produce significant effects in some prior studies). Only two menstrual cycle studies have confirmed the occurrence of ovulation during the high fertile testing phase, but they were studies of female sexual interest across the cycle (Gangestad et al., 2002; Bullivant et al., 2004), not of visual preferences. No visual preference study of either symmetry or masculinity has yet provided direct evidence of ovulation occurring in their female "high fertile" participants. The present study is therefore the first mate-preference study to employ ovulation predictor kits to ensure that women were correctly classified at high fertility, and also to allow the exclusion of anovulatory cycles.

In order to maximise differences in fertility between the two testing sessions, women in our study were tested at ovulation and during the luteal phase (approximately one week after ovulation), and prior to the onset of next menses. Testing at these two session times also maximises differences between progesterone levels during the menstrual cycle (Gilbert, 2000; and see Jones et al., 2005a; Jones et al., 2005b), in case preference shifts are directed at finding a good parent rather than good genes. Women

with regular menstrual cycles rated male face and body photographs for attractiveness in terms of a short-term sexual partner, at high and low fertile days of the menstrual cycle. Short-term attractiveness ratings were targeted because previous research has shown a cyclic shift in short-term, but not long-term partner judgments (Penton-Voak et al., 1999). Masculinity and symmetry ratings were obtained from a previous study (Peters et al., 2008). These ratings were made by different groups of female raters, most of whom were using hormonal contraceptives which eliminate any cyclic effects (Penton-Voak et al., 1999; Little et al., 2002). We correlated high and low fertile attractiveness ratings with these independent ratings of masculinity and symmetry and preference strengths at the high and low fertile phase were compared.

The current study aimed to test whether women's mate choice preferences change over the menstrual cycle in a biologically relevant context and using strict criteria to confirm high fertility testing dates. Using computer-generated stimuli, previous studies have found an increase in visual preferences at high fertility for masculinity, and have reported inconsistent results for symmetry. Our investigation of cyclic shifts in preferences for symmetry and masculinity in male faces and bodies is the first to a) use unmanipulated photographs of individual males, b) confirm the occurrence of ovulation in our high fertility testing sessions and, c) investigate body preferences for symmetry during the menstrual cycle. If evidence for a shift in symmetry or masculinity preference can be shown using photographs of real faces and bodies, this would provide strong evidence that a change in visual preferences throughout the menstrual cycle can be generalised to actual human mate choice.

### **3.3 METHOD.**

#### **3.3.1 RATERS.**

Twenty-seven Caucasian females with regular menstrual cycles participated. Participants were not currently using any form of hormonal contraception. Two of these females did not ovulate and were excluded from analyses. The mean age of the remaining 25 participants was 28.9 years (S.D. = 3.4, range = 23-34 years) and 80% of these women were in a stable relationship at the time of testing. Females in this sample had a mean cycle length of 29 days (S.D. = 1.9, range = 25-32 days).

#### **3.3.2 STIMULI.**

Front-view face and body colour photographs of 119 adult caucasian males were used as stimuli for the attractiveness ratings (Peters et al., 2008) (Figure 1). In the body photographs, the men wore white fitted singlets and shorts and stood with arms relaxed by their sides. Face photographs displayed a neutral facial expression, and were cropped so that most hair cues were removed. Photographs were presented on a computer screen at 72 pixels per inch, with a constant height (320 pixels for faces and 480 pixels for bodies) and varying width.

### 3.3.3 PROCEDURE.

Participants rated the face and body photographs for attractiveness at high and low fertile points of the menstrual cycle. Each participant used an *Ovuplan* (Key Pharmaceuticals) or *Confirm* (Mentholatum) ovulation predictor kit that determines a surge in luteinizing hormone (LH): the hormone that triggers ovulation. Within 48 hours of the LH surge, females rated the faces and bodies for attractiveness. Women were therefore tested on the day before, or the day of ovulation, when the probability of conception is highest (Wilcox et al., 1995). This was termed the “high fertility” testing session.

Females also rated the faces and bodies for attractiveness during the luteal phase of the menstrual cycle. This phase occurs after ovulation but before the onset of menses, and is associated with a very low chance of pregnancy (henceforth termed the “low fertility” testing session). Order of testing was balanced across participants (half first rated the images at ovulation and during the luteal phase second and half vice versa).

The faces and bodies were rated for attractiveness on a 7-point Likert scale (1=not attractive at all, 7=very attractive). Females were asked to rate in terms of sexual attractiveness, as if they were rating a potential short-term partner, and were encouraged to use the full range of the rating scale. The photographs were blocked by image type (face or body) and presented randomly within each block. Order of image type presentation was also balanced, with half of the participants in each testing order (ovulation-luteal or luteal-ovulation) rating faces first and bodies second, and half vice versa. Images remained on the screen until a rating was made. There was very high agreement on attractiveness ratings between raters with all Cronbach alphas  $> 0.95$  ( $M = 0.95$ ,  $S.D. = 0.01$ ).

Separate ratings of masculinity and symmetry were taken from Peters et al.

(2008). These ratings were made by two independent groups of 12 women who rated the face and body photographs only once, following the same method as outlined above. Of these women, 88% were on the pill and the remainder participated on no specific day of their menstrual cycle. Because most of the masculinity and symmetry raters were taking hormonal contraceptives, no cyclic effects were expected in these rater groups (Penton-Voak et al., 1999; Little et al., 2002). As for the attractiveness ratings, mean Cronbach alphas for face and body masculinity and symmetry were high (masculinity  $M = 0.91$ ,  $S.D. = 0.04$ , symmetry  $M = 0.73$ ,  $S.D. = 0.06$ ).

#### 3.3.4 STATISTICAL ANALYSES

First, low fertility face, low fertility body, high fertility face, and high fertility body attractiveness ratings were calculated for each female rater by averaging across all male faces and all male bodies. We then performed a within-subject comparison of the high and low fertility ratings to assess whether attractiveness ratings changed across the menstrual cycle. Second, ratings were averaged across female raters to provide high and low fertility ratings of attractiveness for each individual male face and body. Correlations between masculinity and attractiveness at high fertility were compared with those at low fertility, and the same was done for ratings of symmetry.

### 3.4 RESULTS.

There was no significant difference in attractiveness ratings made at high and low fertility phases of the cycle for either faces  $t_{24} = -0.20$ ,  $p = 0.85$  (high fertility face rating:  $M = 3.3$ ,  $SE = 0.07$ ; low fertility face rating:  $M = 3.3$ ,  $SE = 0.1$ ) or bodies  $t_{24} = 0.23$ ,  $p = 0.82$  (high fertility body rating:  $M = 3.6$ ,  $SE = 0.09$ ; low fertility body rating:  $M = 3.7$ ,  $SE = 0.09$ ).

Further analyses were conducted using attractiveness ratings for the male faces and bodies, averaged across female raters so that these attractiveness ratings could be correlated with masculinity and symmetry ratings that had already been collected for the males' photographs. Descriptive statistics for attractiveness, masculinity and symmetry ratings of each male face and body are shown in Table 1. Both face and body masculinity were significantly correlated with low and high fertility attractiveness ratings (Figures 2 & 3). Similarly, face and body symmetry were also significantly correlated with attractiveness rated at both low and high fertility, although the correlations were lower than those for masculinity (Figures 2 & 4).

We formally compared high and low fertility preferences for masculinity and

symmetry following Cohen and Cohen's (1983) method for comparing dependent correlations which involve a shared variable. There was no significant difference between the high and low fertility preferences for masculinity in faces ( $t_{114} = 0.07, p = 0.94$ ) or bodies ( $t_{114} = -0.44, p = 0.65$ ). Nor was there any significant difference found between at high and low fertility preferences for symmetry (Faces:  $t_{114} = 0.91, p = 0.37$ ; Bodies:  $t_{114} = -0.45, p = 0.66$ ).

### 3.5 DISCUSSION.

This is the first study to use natural photographs of individual men to investigate women's visual preferences over the menstrual cycle. It is also the first to assess preferences for body symmetry across the cycle, and the first to confirm the occurrence of ovulation during high fertility testing sessions. Our results showed no significant difference between attractiveness ratings made at high and low fertility phases of the menstrual cycle, and provide no evidence for a cyclic change in preference for either masculinity or symmetry in photographs of male faces or bodies. Correlations between attractiveness and masculinity, and attractiveness and symmetry did not differ significantly between ovulatory and luteal phase rating sessions. While our results add to the body of literature that finds no evidence for a shift in visual preference for facial symmetry (see Koehler et al., 2002; Cardenas & Harris, 2007; Oinonen & Mazmanian, 2007), they are in contrast to findings by Little et al. (2007b) who found an increased facial symmetry preference during the fertile phase. Our results are also contrary to several studies which find an enhanced preference for masculinity when conception is likely for faces (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001) and bodies (Little et al., 2007a).

Given the numerous studies that have found evidence for an increased preference for masculinity, our results are perhaps surprising. It is unlikely that our testing method did not have the power to detect any changes in preferences. Our study was based on ratings of a relatively large number of stimuli (faces  $N=117$ , bodies  $N=117$ ) compared with previous studies (e.g. Penton-Voak & Perrett, 2000,  $N=5$ , Penton-Voak et al. 1999,  $N_{study\ 1}=10$  &  $N_{study\ 2}=5$ , Johnston et al. 2001,  $N=1$  continuum), and there was good variance within our ratings. While our female sample size ( $N=25$ ) was lower than that of previous studies (e.g. Penton-Voak & Perrett, 2000,  $N=139$ , Penton-Voak et al. 1999,  $N_{study\ 1}=35$  &  $N_{study\ 2}=65$ , Johnston et al. 2001,  $N=42$ ), our Cronbach alphas show very high agreement between raters ( $>0.95$ ), which indicates that

the inclusion of more female raters is not likely to have altered the outcome of our study.

We also maximised the chances of detecting cyclic changes, if any were present, in several ways. The menstrual cycle shift in masculinity preferences is stronger for short-term partner preferences (Penton-Voak et al., 1999; Johnston et al., 2001; Pawlowski & Jasienska, 2005), and is also stronger for women in relationships (Havlicek et al., 2005). Our female participants rated male attractiveness in terms of a short-term partner, and 80% were in stable relationships at the time of testing: conditions that would have maximised any detectable cyclic shift in preferences. In addition, classification of female participants into low and high fertility was strictly controlled to enable maximal differences in fertility between testing sessions. Taken together, the use of ovulation predictor kits, short-term partner attractiveness ratings, and the relationship status of the majority of the women should have increased the likelihood of finding cyclic shifts in female mate preferences, and still none were evident.

Although findings from prior studies of visual preferences for masculinity during the menstrual cycle are robust, our study suggests that the menstrual cycle effect may be contingent on the use of computer-generated faces or bodies. Each study that found an enhanced visual preference for masculinity during ovulation, presented experimental stimuli that were generated to vary only in masculinity levels (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Little et al., 2007a). The artificial stimuli employed might enhance the detection of a preference shift above what might be evident in natural populations, because of the uni-dimensional face variation.

There is some evidence that symmetry detection may improve around ovulation, compared with the luteal phase (Oinonen & Mazmanian, 2007), but a similar increase in symmetry preferences is less clear. Although one study has found an increase in facial symmetry preferences around ovulation using the computer-generated stimuli method (Little et al., 2007b), three other studies that used similar methodologies found no evidence for a cyclic shift in symmetry preferences (Koehler et al., 2002; Cardenas & Harris, 2004; Oinonen & Mazmanian, 2007). Our study using natural images adds to the converging evidence against cyclic shifts in symmetry preferences and suggests that even when a shift is found, the change in preference may not be biologically relevant.

Although our results suggest that there is no cyclic shift in visual preferences for

symmetry, there is, nevertheless, evidence for an increase in preference for the smell of symmetric men at the fertile point of the menstrual cycle (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999b; Thornhill et al., 2003). This may be because women develop a more sensitive sense of smell during ovulation (Doty et al., 1981), which may allow them to assess subtle cues which may not be evident during other times of the cycle.

The present findings have implications for understanding human mate choice. Attractiveness ratings for this set of male faces are correlated with their mating success (Peters et al., 2008), which suggests that ratings provide information about actual mate choice. Our results raise doubts over whether changes in visual preferences during the menstrual cycle affect mate choice.

Using photographs of real male faces and bodies that vary on numerous dimensions simultaneously, we found that preferences for masculinity and symmetry remained the same during ovulation and the luteal phase. A consistent, strong preference for masculinity may reflect a preference for a healthy mate (Rhodes et al., 2003) which would confer benefits to the female whether or not she is at the fertile point of her cycle. Similarly, a consistent preference for symmetry in a potential mate throughout the menstrual cycle may also be adaptive. Higher levels of symmetry are thought to result from an ability to withstand exposure to pathogens and toxins, because of “good genes” (Thornhill & Gangestad, 1999a). A partner with good genes may not only provide indirect benefits via the production of superior offspring, but may also offer direct benefits if good genes are associated with lower contagion, which would be advantageous to a female at any point of the cycle.

In summary, although there is strong evidence for an increase in preference for masculinity during high fertility days of the cycle in studies using artificial stimuli, this study suggests that the menstrual cycle shift may not affect preferences for real faces and bodies. This study also found no evidence for a shift in face and body symmetry preferences, which replicates most previous studies of visual preferences for symmetry. These results suggest that the subtle menstrual cycle shifts found in studies using computer-generated stimuli may not influence actual female mate choice. Preferences for masculinity and symmetry are equally strong at both high and low fertility phases of the menstrual cycle. This study highlights the importance of using experimental procedures that reflect biologically relevant decisions.

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Table 1. Mean ( $\pm$  S.D) female ratings of male faces and bodies for all appearance variables.

	Male Faces (N=117)	Male Bodies (N=117)
Attractiveness – High fertility	3.2 (1.0)	3.7 (1.1)
Attractiveness – Low fertility	3.2 (1.0)	3.6 (1.1)
Masculinity	4.1 (1.0)	4.2 (1.2)
Symmetry	4.1 (0.9)	4.2 (0.8)

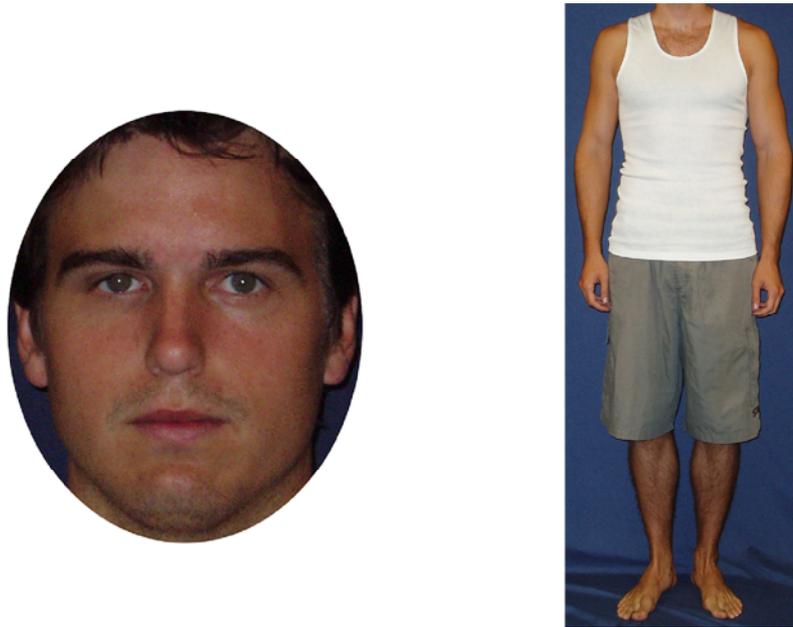


Figure 1. Example of male face and body photographs presented for attractiveness rating at high and low fertile points of the menstrual cycle.

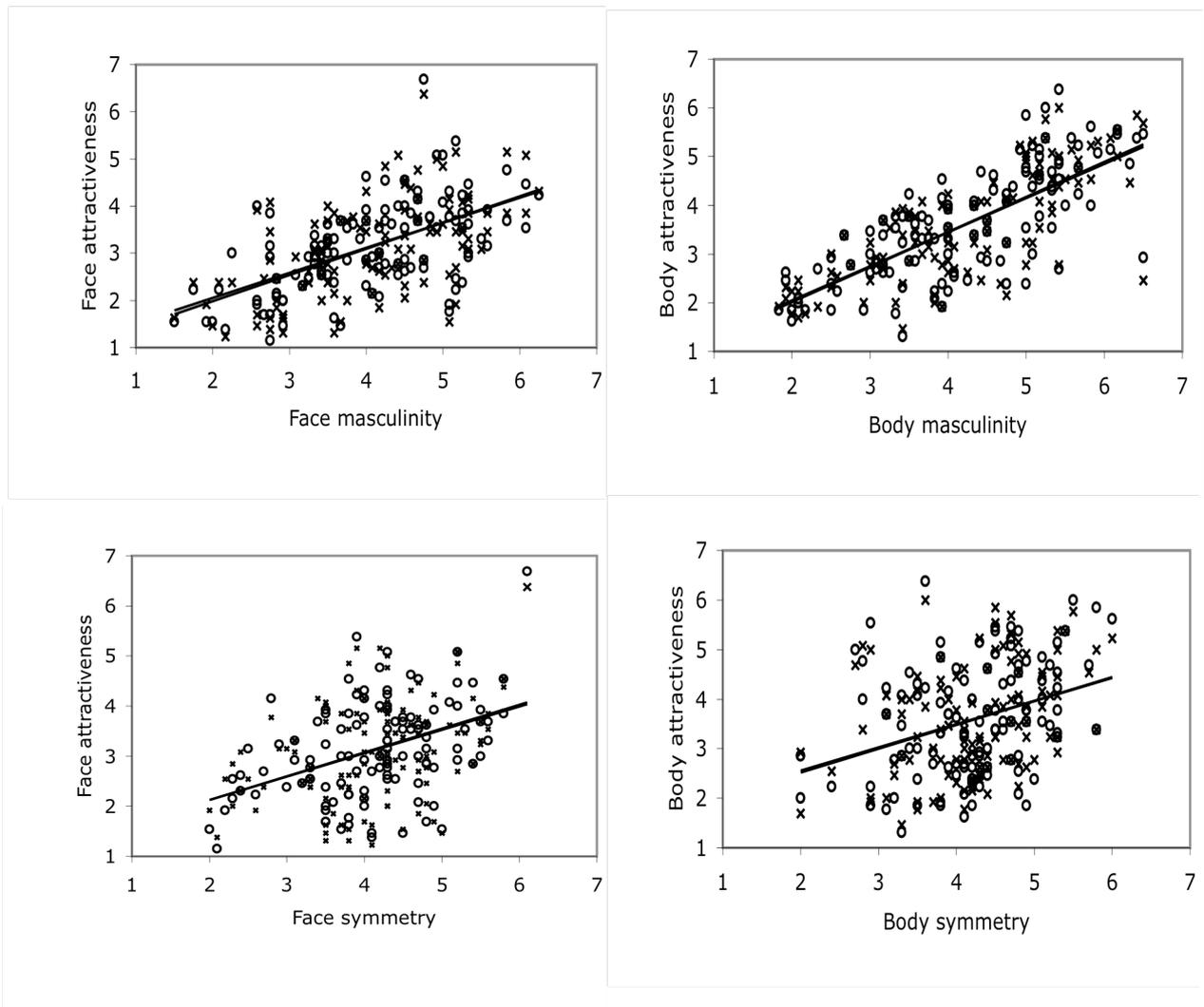


Figure 2. Scatterplots for high and low fertility ratings of attractiveness versus masculinity (top row) and symmetry (bottom row) for faces (left) and bodies (right). Lines of best fit are shown for both low and high fertility ratings, however they overlap in each case.

× = low fertility ratings  
 ○ = high fertility ratings

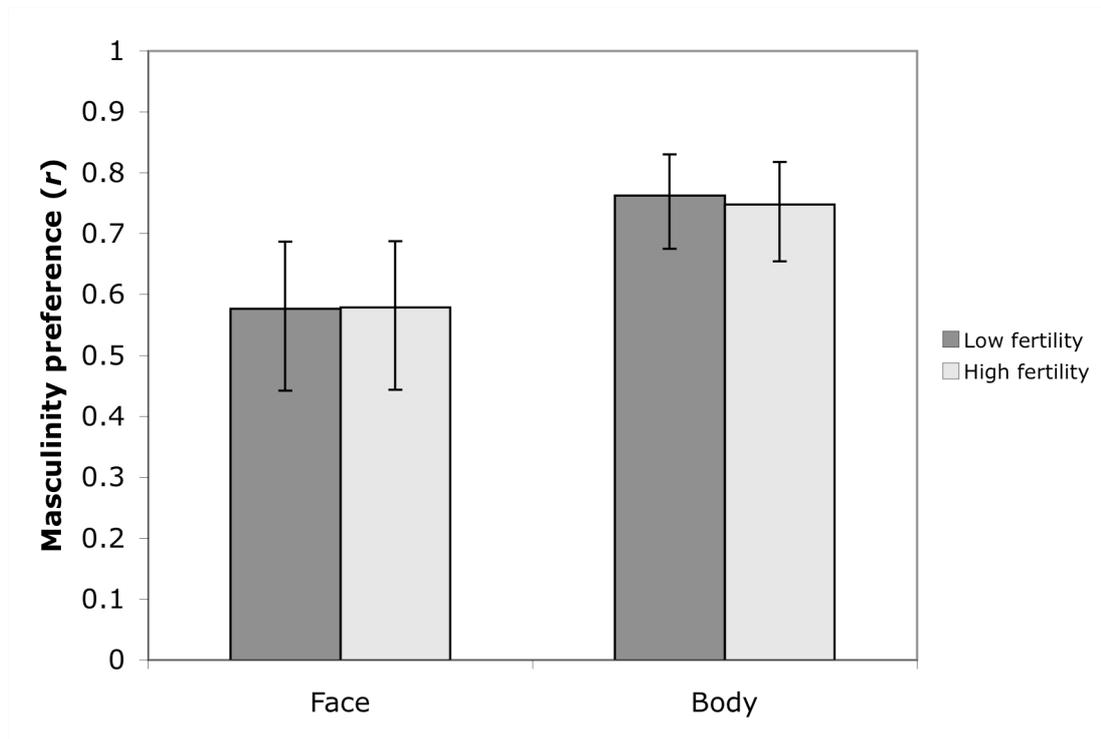


Figure 3. Masculinity preference strength as measured by Pearson correlation coefficients between attractiveness and each of face and body masculinity rated by women at high (dark bars) and low (light bars) fertile points of the menstrual cycle (n=117, all  $p$  values < 0.001). 95% CIs are shown.

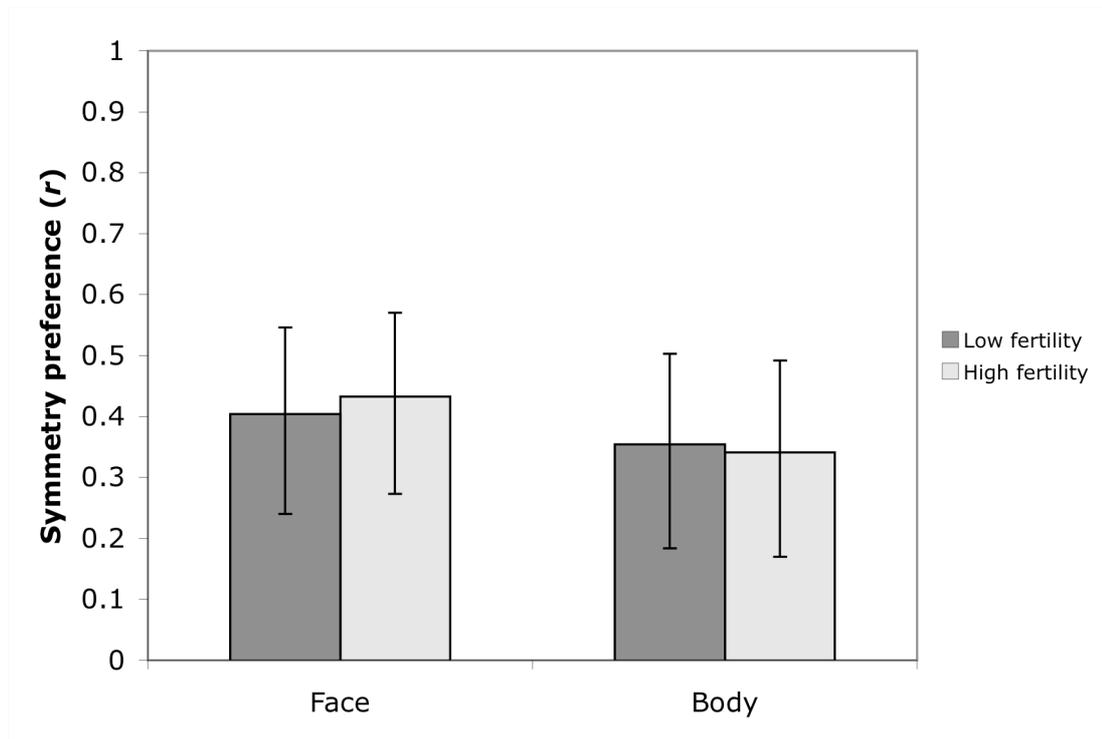


Figure 4. Symmetry preference strength as measured by Pearson correlation coefficients between attractiveness and each of face and body symmetry rated by women at high (dark bars) and low (light bars) fertile points of the menstrual cycle ( $n=117$ , all  $p$  values  $< 0.001$ ). 95% CIs are shown.

## **CHAPTER FOUR**

**TESTOSTERONE IS ASSOCIATED WITH MATING SUCCESS  
BUT NOT ATTRACTIVENESS OR MASCULINITY IN HUMAN  
MALES.**

# **CHAPTER FOUR: TESTOSTERONE IS ASSOCIATED WITH MATING SUCCESS BUT NOT ATTRACTIVENESS OR MASCULINITY IN HUMAN MALES.**

## **4.1 ABSTRACT**

Testosterone (T) is thought to mediate a trade-off between paternal effort and mating effort, such that males investing monogamously have lower T than those with multiple partners. This suggests that high-T males may have a reproductive advantage over their low-T counterparts via increased mating success. This study tested 119 adult males to assess whether T is associated with mating success, and rated masculinity and attractiveness. We found a significant positive correlation between T and cumulative mating success. There was, however, no correlation between T and rated masculinity or attractiveness. This study indicates that although current levels of T covary with male mating success, this effect may not be mediated by women's preferences for visual cues to T levels conveyed in static face or body features. If the T-mating success link is driven by female choice, this effect may be behaviourally modulated, for example, through the augmentation of male mate-seeking or courtship effort.

## 4.2 INTRODUCTION.

Work with non-human animals suggests that T mediates a trade-off between paternal effort and mating effort, such that males investing monogamously have reduced T (e.g. McGlothlin et al., 2007). A T-mediated trade-off between mating effort and parental effort may also characterise humans (see Archer, 2006 for a review). Archer (2006) proposes that differences in T are associated with differing life-history strategies: one that favours mating effort and another that favours parenting effort. Those individuals who favour mating effort over parenting effort will show higher levels of T (Archer, 2006). In males, increased mating effort, at the expense of parenting effort, has significant potential benefits as total reproductive success tends to increase with mating effort (Trivers, 1972; Wade & Shuster, 2002). One measure of mating effort in young adult males is their mating success as measured by the number of sexual partners they have acquired. We therefore suggest that there may be a link between adult T levels and number of sexual partners, and directly investigated whether current (adult) levels of T are associated with cumulative male mating success.

Recent research does suggest that T may be associated with mating strategy and relationship status in humans (Gray et al., 2002; McIntyre et al., 2006; van Anders et al., 2007; van Anders & Watson, 2007). Specifically, men in monogamous relationships have lower T than single men (McIntyre et al., 2006; van Anders & Watson, 2007) and men with multiple partners (van Anders et al., 2007). Furthermore, men who are fathers have lower T than single men, and trade off mating effort for parenting effort (Gray et al., 2002). Thus, it appears that high-T men may favour a multiple-mate or short-term mating strategy. These men, who are not committed to a single relationship, therefore have the opportunity to acquire more sexual partners than men with a monogamous partner.

Adult T levels may be associated with behaviour and mating success, either by motivating, or fluctuating in response to, certain behaviours. Testosterone has been shown to affect sexual motivation in males. High T motivates sexual activity in adolescent boys (Udry et al., 1985; Udry, 1988; Halpern et al., 1993), increases extra-pair interest and decreases commitment to monogamous relationships in men (McIntyre et al., 2006). Testosterone replacement studies of hypogonadal men have also shown that T plays an important role in sexual desire and interest (see Sherwin, 1988 for a review). These same studies, however, suggest that there may be an upper threshold beyond which increases in T cease to have behavioural effects (Sherwin, 1988; see also

Wingfield et al., 1990). Fluctuations in T levels have nevertheless been shown to account for variations in sexual activity within individuals (Hirschenhauser et al., 2002) although variation between individuals is not associated with variation in sexual activity over a short period of time (Brown et al., 1978). The association between testosterone and behaviour can manifest equally in the opposite direction, whereby certain behaviours, particularly in the context of reproduction, can cause an increase in T, for example in response to “challenges” (Archer, 2006) and interactions with women (Roney et al., 2003).

An association between T and a successful short-term mating strategy may be augmented via a female preference for males with high T. Testosterone is associated with the development of secondary sexual characteristics in males (Enlow, 1990), and many studies have shown that females find these traits attractive (Rhodes, 2006), arguably because they are honest signals of male health and vigour that reflect an individual’s ability to withstand the associated costs of T (Folstad & Karter, 1992).

In many vertebrate species, T is related to the expression of characteristics used for signalling to potential mates. For example, birds and fishes are two groups that utilise bright red and orange colours to attract mates (Brush, 1978; Jayasooriya et al., 2002; Blount et al., 2003). In humans, the link between T and masculinity is less clear. The development of masculine traits is stimulated by androgens during adolescence (Tanner, 1989; Enlow, 1990), although there is little correlation between adolescent and adult T levels ( $r$  varies between 0.02 and 0.05) (van Bokhoven et al., 2006). Therefore, although masculine traits in adult males are generally attractive to females (Rhodes, 2006) and may provide insights as to the condition of the male during puberty (Rhodes et al., 2003), it is unlikely that they convey any information regarding *current* T levels or immunocompetence to a potential mate. Nevertheless, several studies have investigated whether masculinity or attractiveness are associated with current T levels. Most found no association between attractiveness and T (Swaddle & Reiersen, 2002; Neave et al., 2003; Penton-Voak & Chen, 2004; but see Roney et al., 2006). Furthermore, while Penton-Voak and Chen (2004) found a weak link between masculinity and T, studies by Bogaert and Fisher (1995) and Neave et al. (2003) found no such link using a direct correlational approach.

Bogaert and Fisher (1995) have previously reported a significant correlation of 0.2 between T and current cumulative number of sexual partners, and no significant correlation between T and attractiveness. However, their measures of T were taken in

the afternoon, when participant T levels are likely to have been affected by behavioural interactions and activities, such as those discussed above. Furthermore, in Bogaert and Fisher's (1995) study ratings of attractiveness were made by only one male and one female. These ratings were combined to provide an aggregate attractiveness score that yielded a Cronbach's alpha of just 0.56. Therefore these ratings were arguably unreliable, and additionally did not represent attractiveness judgements that are most relevant to mating success: opposite-sex ratings. The current study aimed to replicate Bogaert and Fisher's findings, using improved methods for assessing T levels and attractiveness.

The main aim of this study was to investigate the association between T and mating success in humans. We measured salivary T levels from samples provided upon waking, for a sample of male undergraduate students who completed self-reported surveys of their sexual behaviour. If T is associated with a propensity for increased mating effort, as predicted by Archer (2006) then we expect that higher T will be associated with higher total number of sexual partners (i.e. have increased mating success). We also examined the associations between T and attractiveness and masculinity of both faces and bodies. Both faces and bodies are important for human mate choice (Peters et al., 2007), yet studies have previously focussed only on ratings of facial attractiveness and masculinity. We are the first to include female ratings of body, as well as face, appearance in our study of the relationship between T and appearance. Attractiveness and masculinity were rated by two independent groups of 12 females, and correlated with T measurements to determine whether female perceptions of visual cues to T could account for any relationship between T and mating success.

### **4.3 METHOD.**

#### **4.3.1 PARTICIPANTS.**

Participants were recruited from the University of Western Australia. One hundred and nineteen males participated (Mean age 22.5, S.D. 4.9, range 18-35 years), in return for course credit or remuneration for travel expenses. All males were heterosexual, Caucasian and cleanly shaven.

#### **4.3.2 PARTICIPANT PROCEDURE.**

Each male participant was photographed wearing a white fitted singlet, and dark coloured shorts. Both full-length body and close-up face photos were taken. The

participants were asked to adopt a neutral expression and to stand with their feet slightly apart, with their arms relaxed by their sides.

Each participant completed a sexual history questionnaire, based on that used by Rhodes et al. (2005). In this questionnaire, individuals were asked their age at first intercourse and the total number of sexual partners. This value was sub-categorised into the number of relationships that were: “one night stands”; between 1 day and 1 month (short-term); longer than one month but less than one year (mid-term), and longer than one year (long-term). Participants were also asked on how many occasions they had had sexual intercourse with a third party while in a relationship with their partner (“cheating”) and on how many occasions they had had intercourse with someone they knew to be in a relationship with somebody else (“poaching”).

Participants also provided a 5mL saliva sample for T assay. They were given a plastic vial with 5mL marked on the outside and some sugarless chewing gum. Participants were instructed to chew the gum immediately after waking in the morning, to stimulate saliva production, and to fill the vial to the marked line with saliva. Morning samples were collected because baseline T secretion follows a circadian pattern with levels maximal in the morning (Dabbs, 1990). Male T levels have also shown transient increases after even brief interactions with both men and women, with a latency period of approximately 20 minutes (Roney et al., 2003), therefore, saliva collection upon waking also controlled for short term hormonal responses to interactions such as these. Samples collected were therefore comparable across participants because they represented individual differences between maximum baseline T levels that were unaffected by behavioural interactions. Saliva samples were delivered to the lab within 2 hours of collection and frozen immediately at -80°C. Although multiple saliva samples might have increased the reliability of T measurements (Dabbs, 1990), single sample salivary T levels have been used widely to assess relationships between T, and masculinity and attractiveness (Neave et al., 2003; Penton-Voak & Chen, 2004; Roney et al., 2006), and courtship/mating behaviour (Halpern et al., 1998; Gray et al., 2002; Burnham et al., 2003; Roney et al., 2003; Gray et al., 2006; McIntyre et al., 2006; van Anders et al., 2007; van Anders & Watson, 2007).

#### 4.3.3 SALIVARY TESTOSTERONE.

All saliva samples were sent to Analytical Reference Laboratories Pty Ltd (ARL) in Melbourne, Australia, for T assay by ELISA technique. Twenty of these

samples were sent to a second independent laboratory (Canterbury Health Laboratories (CHL), in Christchurch, New Zealand) and an analysis of repeatability was performed. Testosterone assays were highly repeatable ( $R=0.806$ ,  $F_{18,19}=5.145$ ,  $p=0.004$ ). Intra-assay coefficients of variation for the method used by CHL were 7.6, 9.8 and 12.0% respectively, for 4.3, 13.8 and 22.7 nmol/L respectively, and inter-assay variations did not exceed 12.5% (Elder & Lewis, 1985). For this method, average T recovery within the range of 2-25nmol/L ranged from >90% to < 110%.

To control for possible confounding factors associated with lifestyle that were indicated in the T literature, we ran a general linear model with T as the dependent variable and lifestyle factors regarding drug use, exercise, illness and exposure to toxins entered as independent variables. Each non-significant variable was removed by step-wise deletion, and the model was re-run at each step until only significant variables remained. The final model was significant ( $F_{10,96}=3.45$   $p<0.001$ ). Variables remaining that decreased T were: bipolar disorder ( $F_{1,96}=5.23$   $p=0.02$ ), zinc ( $F_{1,96}=4.38$   $p=0.04$ ) or iron ( $F_{1,96}=5.13$   $p=0.03$ ) supplements. Variables remaining that increased T were: currently taking pain medication ( $F_{1,96}=5.53$   $p=0.02$ ), frequency of marijuana use ( $F_{4,96}=3.09$   $p=0.02$ ), length of time marijuana had been used ( $F_{1,96}=6.60$   $p=0.01$ ), and length of time cigarettes had been used ( $F_{1,96}=5.53$   $p=0.02$ ). The residuals from the final model were highly correlated with the raw T values ( $r = 0.88$ ,  $n = 107$ ,  $p < 0.001$ ) and were used for subsequent analyses as the “T” variable, to control for lifestyle factors. A single multivariate model that included lifestyle factors might have been preferable. However, sexual behaviour data were severely left-skewed, and could not be normalised by any transformation, violating the assumptions of a parametric model. By using residuals we were able to perform non-parametric Kendall’s Tau partial correlations that allow partialling out of only one covariate. We controlled for age because of its significant effect on cumulative mating success.

#### 4.3.4 RATINGS.

As both face and body attractiveness contribute to overall attractiveness (Peters et al., 2007), which is generally most relevant to partner choice, ratings for both were collected. Each face and body image of the male participants was rated for attractiveness and masculinity on a seven-point scale (1= not attractive/masculine; 7 = very attractive/masculine) as in Rhodes et al. (2005). As in previous studies (e.g. Rhodes et al., 2005; Peters et al., 2007), the height of the body photos was held constant (width varying) which minimised information about male height available to the female

raters. Female raters were recruited from the same university pool as the male sample. Of these women, 88% were taking hormonal contraceptives that minimised any potential menstrual cycle effects on ratings (see for example Penton-Voak & Perrett 2001, Penton-Voak & Perrett, 2001). Twelve females rated the images for attractiveness (mean age = 19.9, SD = 3.8, range = 18-28 years) and another 12 rated them for masculinity (mean age = 25.5, SD = 4.4, range = 18-32 years). Inter-rater agreement was high (coefficient alpha for attractiveness = 0.90 and masculinity = 0.90). If a participant recognised a face in the set of photographs, their ratings of that face, and corresponding body, were excluded (mean number of recognised males = 1.2 per rater). An attractiveness and masculinity score was calculated for each face and body, by averaging across raters.

#### **4.4 RESULTS.**

We analysed sexual behaviour in two ways. The first was a raw count of the cumulative number of sexual partners, and the second was a composite score incorporating the various types of relationships reported. Although sexual behaviour data were left-skewed, a principal components analysis can be appropriately used on non-normal data to describe relationships between variables (Tabachnick & Fidell, 2007), and was performed on the following sexual behaviour variables: age at first sex, total number of sexual partners, one night stands, short-term partners, mid-term partners, long-term partners, cheating, and poaching. One principal component was extracted, which accounted for 49.2% of the variance in sexual behaviour and loaded positively on all variables except age at first sex (Table 1). This component was used as a “mating success” variable in subsequent analyses. By incorporating information about the nature and length of each relationship, this variable arguably explains more about mating success than a simple count of partner numbers.

As for the original variables, the mating success PC was not normally distributed. Furthermore, both number of sexual partners and mating success were significantly correlated with age (sexual partners  $\tau_{113}=0.35$ ,  $p<0.001$ , mating success  $\tau_{113}=0.39$ ,  $p<0.001$ ). Therefore, Kendall’s Tau non-parametric partial correlations, controlling for age, were used to examine the relationships between sexual behaviour and T. We found a small, but significant, correlation between T and number of sexual partners, when controlling for age ( $\tau_{107}=0.11$ ,  $p<0.05$ ). This correlation remained the same when our mating success variable was analysed instead of number of sexual

partners ( $\tau_{107}=0.11$ ,  $p<0.05$ ). When raw T values were analysed instead of residuals from our GLM that controlled for life-style variables, the correlation between T and mating success was of a similar magnitude but was not significant ( $\tau_{107}=0.08$ , n.s.).

All appearance variables were tested for normality prior to statistical analysis. Face and body attractiveness scores were log transformed to achieve normal distributions. Masculinity scores were normally distributed. Face and body attractiveness were highly correlated with each other and with face and body masculinity (Table 2). To reduce the number of variables in our analyses, principal components analyses were conducted on face and body attractiveness ratings and on face and body masculinity ratings. Each PCA yielded a single principal component: overall attractiveness (eigenvalue = 1.49; variance explained = 74.5%; eigenvector face = 0.71, body = 0.71) and overall masculinity (eigenvalue = 1.47; variance explained = 73.4%; eigenvector face = 0.71, body = 0.71). These overall attractiveness and masculinity PC scores were used in subsequent analyses.

Pearson correlations were used in order to assess the relationships between T, attractiveness and masculinity. Masculinity, but not attractiveness, was correlated with age (masculinity  $r = 0.37$ ,  $n = 112$ ,  $p < 0.001$ ; attractiveness  $r = -0.07$ ,  $n = 112$ ,  $p = 0.441$ ), so partial correlations, controlling for age were used for correlations involving masculinity. Attractiveness and masculinity were significantly correlated with each other (*partial*  $r = 0.75$ ,  $n = 106$ ,  $p < 0.001$ ), and both were significantly correlated with mating success, controlling for age (attractiveness *partial*  $\tau_{112}=0.13$ ,  $p<0.05$ ; masculinity *partial*  $\tau_{112}=0.17$ ,  $p<0.01$ ), replicating previous findings (Rhodes et al., 2005). Importantly, however, T (controlling for lifestyle factors) was not correlated with either attractiveness ( $r = -0.12$ ,  $n = 106$ ,  $p = 0.22$ ) or masculinity (*partial*  $r = -0.01$ ,  $n = 106$ ,  $p = 0.94$ ). These findings were unchanged if raw T scores were used in the correlations. The 95% confidence intervals for the observed correlations were calculated to assess the robustness of these null results. In the case of the correlation between T and attractiveness, the correlation was more likely to be negative than positive (-0.31, 0.07), a trend in the opposite direction to that predicted, and in the case of the correlation between T and masculinity, the CIs were symmetrical about zero (-0.20, 0.18), suggesting that the null hypothesis is likely to be true.

#### **4.5 DISCUSSION.**

Controlling for age, we found that T varied positively with cumulative number of sexual partners, and with our composite mating success variable that incorporated more information about the nature of each reported sexual relationship (for subsequent discussion, both of these terms will be collectively referred to as mating success). Although not strong relationships, these results do suggest that T may be subject to sexual selection if males with higher mating success also have a higher reproductive success as suggested by Trivers (1972). The relationship between T and mating success was only significant when controlling for lifestyle factors that impact on hormonal profiles. The presence of factors such as medication and drug use in male participants may therefore mask any true effect of T on behaviour. Accordingly, previous studies investigating relationships between T and behaviour, which did not control for such factors, may have underestimated the relationship.

It is difficult to deduce the direction of causality that a T-mating-success link might follow in studies of humans, because we are limited to a correlational approach. We recognise that it is impossible to conclude cause and effect from correlational studies such as ours, and cannot rule out an increase in baseline T in response to higher mating success. Indeed increased sexual experience has been shown to cause increases in T levels in humans (Kraemer et al., 1976; Hellhamer et al., 1985; Roney et al., 2003) and other animals (e.g. birds, Wingfield et al., 1990). Nevertheless, we also note that baseline T levels are heritable (Meikle et al., 1988), suggesting that they represent an intrinsic property of individual men that is capable of responding to selection. Furthermore, in studies of non-human animals, long-term implantation and experimental manipulations of T, which allow a direct examination of cause and effect, have shown that T generally increases mating effort (Ketterson et al., 1992; Enstrom et al., 1997; Raouf et al., 1997; Cawthorn et al., 1998; Schoech et al., 1998; Reed et al., 2006).

As with all studies of sexual behaviour, there is the potential for self-reported data to introduce some bias to the results. Because self-report is the only way to investigate sexual behaviours in humans, we took care to stress to our male participants the importance of honesty when responding to the questionnaires, and allowed them to complete the questionnaire in privacy to encourage truthfulness. Studies suggest that such protocols improve the accuracy of estimates of sexual behaviour (Eriksen, 1999; Alexander, 2003).

Our results are in concordance with findings by Bogaert and Fisher (1995) who also showed that higher T is associated with the ability to acquire a greater number of female partners in a large sample of adult men. Our study improved on Bogaert and Fisher's by controlling not only for lifestyle factors, but also for behavioural interactions that may cause individual fluctuations in T, for example increases in T in response to competition (see Archer, 2006 for meta-analytic review) or interactions with women (Roney et al., 2003), by collecting saliva samples upon waking.

Archer (2006) suggested that T may be associated with dual mating strategies in humans, one favouring mating effort and the other favouring parenting effort. Our results are consistent with this view, and suggest that high-T males may invest more time and energy into mating effort, which is reflected in a higher cumulative mating success. Other studies also suggest that men with high T show increased mating effort and are less likely to enter into or maintain stable relationships (see for example Booth & Dabbs, 1993; Gray et al., 2002; Burnham et al., 2003; van Anders & Watson, 2007). Indeed, in vertebrates generally, and in mammals particularly, high levels of T are strongly associated with high frequencies of sexual behaviour (Hirschenhauser & Oliveira, 2006). Conversely lower T levels are associated with better paternal care and lowered mating effort (Storey et al., 2000; Berg & Wynne-Edwards, 2001; Fleming et al., 2002; Gray et al., 2002).

We suggest two mechanisms that may facilitate an association between T and mating success via male behaviour and/or female preferences. First, mating success and T may come to be associated through the demonstration of dominant physical behaviours, and male contest competition. The hypothesis that T is associated with dominant behaviour is one that has been tested often (see Mazur & Booth, 1998; Hirschenhauser & Oliveira, 2006 for reviews). In many non-human animals, T is associated with aggressive or dominant behaviours, for example, increased territory size and mate guarding (see Wingfield et al., 2001 for a review). A meta-analysis of human studies found broad support for an association between T and various measures of dominance (Archer, 2006). Thus, mating success may be associated with higher T, because T is associated with male contest competition, either via mate seeking behaviour, or through overt aggressive competition.

A second mechanism by which T may affect mating success is via a female preference for males with high T. Females have been hypothesised to prefer T-dependent traits because they honestly signal mate quality (Thornhill & Gangestad,

1999). We therefore suggest that females may preferentially choose high T males more often as mates, because of the benefits that they may enjoy either directly or through producing better quality, healthier offspring. Because males with high T do have slightly higher mating success, it may be that females are choosing these males more frequently as mates, thus enabling these males to successfully adopt a short-term mating strategy. Females may respond to visual, olfactory, auditory or behavioural cues during mate selection. Our results provide no support for the hypothesis that *visual* cues to T-dependent facial and body characteristics drive the selective advantage associated with T. Despite replicating the finding by Rhodes et al. (2005), that attractive and masculine males have higher mating success, we found no evidence that females were sensitive to, or preferred, visual cues of circulating T in the male face and body, because T did not significantly correlate with either masculinity or attractiveness. Importantly, the current findings do not rule out the possibility that female choice is involved in high-T males gaining more partners. They simply suggest that females may not rely on the limited visual cues available in a static image to do so.

Our results are consistent with those of Neave et al. (2003) who, using a similar ratings method, also found no association between T and masculinity or attractiveness. On the other hand, our results run counter to the findings of Penton-Voak and Chen (2004) who reported a weak, albeit significant, association between T and masculinity (high-T composites were chosen as the more masculine from high- & low-T pairs, 53% of the time). However, these authors note that only men with very high or very low T levels may be distinguishable in terms of masculinity. Taken together, the evidence suggests that current T levels may have little or no relationship with masculinity of appearance. This is perhaps unsurprising considering there is no correlation between adult T levels, and T levels during adolescence when masculine features are developing (van Bokhoven et al., 2006).

In conclusion, the results of this study suggest that adult male T levels are related to mating success, although this relationship is weak. These results support the hypothesis that high T levels are associated with increased mating effort. High-T males therefore have a mating advantage over their lower-T peers. If mating success contributes more to reproductive success than parental investment, T levels could be subject to sexual selection. We found no evidence that T levels were associated with perceived attractiveness based on static photographs, so if the T-mating success link is driven by female choice, this effect is more likely to be behaviourally mediated.

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Table 1. Principal components analysis on sexual behaviour questionnaire variables.

	PC1
Eigenvalue	3.94
Percent	49.21
Eigenvectors	
Age at first sex	-0.026
Number of sexual partners	0.480
Number of one-night stands	0.388
Number of short-term relationships	0.372
Number of mid-term relationships	0.371
Number of long-term relationships	0.313
Cheating	0.365
Poaching	0.336

Table 2. Pearson correlations between face and body appearance variables in males. n = 106 for face variables, n = 107 for body variables.

	Face attractiveness <sup>†</sup>	Body attractiveness <sup>†</sup>	Face masculinity	Body masculinity
Face attractiveness	1	0.488 <sup>***</sup>	0.498 <sup>***</sup>	0.363 <sup>***</sup>
Body attractiveness		1	0.426 <sup>***</sup>	0.692 <sup>***</sup>
Face masculinity			1	0.467 <sup>***</sup>

<sup>†</sup>log transformed values used for face and body attractiveness.

<sup>\*\*\*</sup>p<0.001.

## **CHAPTER FIVE**

# **DOES ATTRACTIVENESS IN MEN PROVIDE CLUES TO SEMEN QUALITY?**

## **CHAPTER FIVE: DOES ATTRACTIVENESS IN MEN PROVIDE CLUES TO SEMEN QUALITY?**

### **5.1 ABSTRACT.**

The psychological mechanisms underlying attractiveness judgements in humans are thought to be evolved adaptations for finding a high quality mate. The phenotype-linked fertility hypothesis proposes that females obtain reliable information on male fertility from male expression of sexual traits. A previous study of Spanish men reported that facial attractiveness was positively associated with semen quality. We aimed to determine whether this effect was widespread by examining a large sample of Australian men. We also extended our study to determine whether cues to semen quality are provided by components of attractiveness: masculinity, averageness, and symmetry. Each male participant was photographed and provided a semen sample that was analysed for sperm morphology, motility and concentration. Two independent sets of women rated the male photographs for attractiveness, and three further sets of twelve women rated the photographs for masculinity, symmetry, or averageness. We found no significant correlations between semen quality parameters and attractiveness or attractive traits. While male physical attractiveness may signal aspects of mate quality, our results suggest that phenotype-linked cues to male fertility may not be general across human populations.

## 5.2 INTRODUCTION.

Attractiveness is associated with mate choice and mating success in humans (Rhodes et al., 2005), and is thought to be an evolved adaptation for finding healthy and fertile mates because attractiveness honestly indicates genotypic and phenotypic quality (Andersson, 1994; Thornhill & Gangestad, 1999). Obtaining a good quality mate may provide genetic benefits or resources that can help to increase an individual's reproductive success. For example, females may acquire indirect genetic benefits for offspring, and/or direct material benefits such as resources and/or parental care (Andersson, 1994; and see Gangestad & Scheyd, 2005 for a review). One direct benefit proposed to be associated with attractiveness is male fertility. The aim of the current study was to examine the association between attractiveness and semen quality in humans, in order to explore whether an attractive male is preferred because of his reproductive potential.

Reproductive health or fertility is perhaps the most important aspect of mate quality, particularly in the context of mate choice, because the ultimate goal of mate selection is to maximise reproductive success. The phenotype-linked fertility hypothesis argues that females can obtain reliable information on male fertility from the expression of male secondary sexual traits (Sheldon, 1994). Although not universal (e.g. Birkhead & Petrie, 1995; Birkhead et al., 1997; Pizzari et al., 2004), some studies have reported positive relationships between attractive male sexual traits and semen quality. For example, in red deer, males with larger antlers produce sperm with greater swimming velocity (Malo et al., 2005). Likewise in guppies, males with greater areas of orange pigmentation produce faster swimming sperm of greater viability (Locatello et al., 2006) (see also Wagner & Harper, 2003; Kortet et al., 2004). For humans, Soler et al. (2003) reported significant correlations between semen quality parameters (sperm motility, morphology and concentration) and facial attractiveness in a sample of 66 adult men. In that study, a second group of women rated a sub-sample of 12 male faces for attractiveness at high and low fertility phases of the menstrual cycle. This sub-sample yielded even higher correlations between attractiveness and semen quality, but there was no difference between the two fertility levels. To date, Soler et al.'s (2003) study has never been replicated, nor has any further data been published on attractiveness and fertility in men. We sought to determine the generality of the

relationship between attractiveness and semen quality in human males by following Soler et al.'s (2003) study using a large sample of Australian men.

Masculinity, symmetry and averageness are three traits that contribute to men's attractiveness to women (Rhodes et al., 2005; Rhodes, 2006). Masculine traits are characterised by a large jaw, prominent brow ridge and cheekbones, while asymmetries arise from deviations from perfect symmetry in bilateral traits (Rhodes, 2006). Average faces and bodies have the arithmetic mean of traits values for a population. Individuals that are high in averageness are low in distinctiveness (Rhodes, 2006). Masculinity, symmetry, and averageness of human faces and bodies are thought to be signals of mate quality in humans (Thornhill & Gangestad, 1999). Masculinity may signal immunocompetence (Folstad & Karter, 1992), and facial masculinity is associated with health during adolescent development in males (Rhodes et al., 2003). Symmetry and averageness are thought to reflect an individual's ability to cope with environmental and genetic stresses throughout development (Fink & Penton-Voak, 2002). In particular, measured body fluctuating asymmetry (FA) has been linked to general health (for a review see Thornhill & Moller, 1997) as well as to semen quality in men (Manning et al., 1998; Firman et al., 2003). The potential for masculinity, symmetry, and averageness to signal aspects of mate quality, and the established link between body FA and semen quality, prompted us to extend our study to investigate the relationships between rated perceptions of these attractiveness traits and semen quality.

To examine the phenotype-linked fertility hypothesis in humans, we assessed semen quality in a large sample of adult males and compared this with ratings of attractiveness. Because both face and body attractiveness contribute to overall attractiveness (Peters et al., 2007), which is generally the most relevant to mate choice, ratings for both were collected and then combined into a single attractiveness component. A number of studies have found increases in female preferences for putative signals of mate quality at the fertile point of the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; DeBruine et al., 2005; and see Puts, 2006 for a review). Like Soler et al. (2003), we therefore included attractiveness ratings from high- and low-fertile points of the menstrual cycle from a second group of females. This additional group of raters also provided an independent set of attractiveness ratings. Our study extends that of Soler et al.'s by using a larger male sample, examining the associations between semen quality and both face and body ratings of

attractiveness, and determining which, if any of the attractive traits masculinity, symmetry, and averageness, are linked with male fertility.

### **5.3 METHOD.**

#### 5.3.1 PARTICIPANTS.

One hundred and eighteen male participants (mean age 22.5, S.D. 4.9, range 18-35 years) were recruited by advertisement at the University of Western Australia. All males were heterosexual and caucasian. An upper age limit of 35 years was set for this study in order to avoid the potential decrease in semen quality that can occur beyond this age (Rolf & Nieschlag, 1997, 2001; Piñón, 2002).

#### 5.3.2 PARTICIPANT PROCEDURE.

Each male participant was photographed wearing a white fitted singlet, and dark coloured shorts. Both full-length body and close-up face photos were taken. The participants were asked to adopt a neutral expression and to stand with their feet slightly apart, with their arms relaxed by their sides.

Each participant completed a questionnaire regarding lifestyle factors that can potentially affect semen quality. This questionnaire was based on that of Kilgallon and Simmons (2005), and contained questions about medications, sedentary patterns, alcohol consumption, cigarette use, illicit drug use, caffeine consumption, weekly sexual activity, location of childhood upbringing, mobile phone placement, dietary habits, and exposure to other environmental factors. Participants also returned self-measured (using vernier callipers) testes dimensions, from which testes volume was calculated using the formula for an ovoid ( $\frac{4}{3} \times \pi \times (\text{length}/2) \times (\text{width}/2)^2$ ). Self-measured testes volume is highly repeatable and provides a good estimate of testes size (Simmons et al., 2004a).

#### 5.3.3 RATINGS OF APPEARANCE VARIABLES.

##### 5.3.3.1 *Attractiveness.*

Female ratings of attractiveness for each male face and body were collected according to the method outlined by Rhodes et al. (2005). The face photograph of one participant was excluded because it was out of focus. Attractiveness was rated on a seven-point scale (1 = not attractive; 7 = very attractive), in the context of a short-term sexual partner, and raters were encouraged to use the whole range of the scale. Photographs were presented in two blocks, one comprising faces only and the other comprising bodies only (randomised within each block), and each photograph remained

on the screen until a rating was made. An attractiveness score for each male face and body was calculated by averaging across all raters. The mean age of the first rater set was 19.9 years (S.D.=3.8, range=17-28,  $N=12$ ). There were no specific participation requirements for these women other than being caucasian and heterosexual, as for to the male sample.

A second set of 27 caucasian, heterosexual females not using any form of hormonal contraception, and with regular menstrual cycles was recruited to rate the photographs for attractiveness at a high- and low-fertile point of the menstrual cycle. Each rater used an *Ovuplan* (Key Pharmaceuticals) or *Confirm* (Mentholatum) ovulation predictor kit that determines a surge in luteinizing hormone: the hormone that triggers ovulation. Two of these females did not ovulate so were excluded from analyses. The mean age of the remaining 25 raters was 28.9 years (S.D.=3.4, range=23-34). During the high-fertile testing session, females rated the faces and bodies within 48 hours of a luteinizing hormone surge, which are the days most likely to result in conception following intercourse (Wilcox et al., 2001). Females were also tested during the luteal phase of the menstrual cycle. This phase occurs after ovulation but before the onset of menses, and is associated with a very low chance of conception. Half of the participants rated the photographs first at ovulation and second during the luteal phase and half vice versa. Inter-rater agreement was very high for both sets of raters, and across ratings made by females tested at high and low fertility (all Cronbach's alphas  $\geq 0.9$ ).

#### 5.3.3.2 *Attractive traits.*

Face and body ratings of attractive traits (masculinity, symmetry, and distinctiveness) were also collected on a seven-point scale using the same method as described above. A verbal description of symmetry and masculinity was given to participants prior to commencement of the testing session. Participants were asked to rate distinctiveness (in terms of "how much would this face/body stand out in a crowd") rather than averageness because it is easier to conceptualise and explain. Distinctiveness ratings were then reverse scored in order to produce averageness scores (i.e. a face given a distinctive score of 1, was reverse-scored to have an averageness score of 7, a distinctiveness score of 2 was reverse-scored as 6, etc). Each of the three appearance variables was rated by a different group of 12 females to ensure each variable was independently assessed. The mean age of all raters was 21.6 years (S.D.=4.9, range=17-34,  $N=36$ ). Inter-rater agreement was high for ratings of face and

body masculinity (Cronbach's alphas  $\geq 0.9$ ) and symmetry (Cronbach's alphas  $\geq 0.7$ ), but lower for distinctiveness (averageness) ratings (face=0.6, body=0.4). A score for each appearance variable was calculated by averaging across raters.

#### 5.3.4 SEMEN ANALYSES.

Each participant was given clear instructions regarding collection of the semen sample. Participants were asked to abstain from intercourse and masturbation for a minimum of 48 hours and a maximum of 6 days prior to providing the sample. The semen sample was collected by masturbation into a sterile vial. Vials were wrapped in insulating foil to maintain temperature, and delivered to the laboratory within 1 hour of collection in order to minimize the risk of reduction in motility over time. Participants were asked to record how long it took to collect their semen sample, the exact time of semen collection, and the time since their previous ejaculation.

Sperm concentration, motility and morphology were assessed according to World Health Organization (WHO) protocol (World Health Organization, 1999). To ensure accurate assessment of semen quality, one of the experimenters (MP) was trained by a qualified seminologist at the Hollywood Fertility Centre (Nedlands, Western Australia) and assessed using the Fertility Society of Australia's External Quality Assurance Scheme for Reproductive Medicine. MP's results fell within the range of results obtained by fertility clinics in the Australasian region.

Immediately after delivery of the semen sample to the laboratory, and following liquefaction, the reduction in viscosity that occurs in normal semen samples within 60 minutes (WHO, 1999), the sample was assessed for motility. A 10 $\mu$ L aliquot was placed onto a slide, with a coverslip and examined under 400x magnification using bright field illumination. One-hundred and thirty spermatozoa per sample were categorized into four motility categories, (A) rapid progressive ( $> 5$  head lengths/second), (B) slow or sluggish progressive, (C) non-progressive but still motile (velocity  $< 5\mu\text{m/s}$ ), and (D) immotile. For further analyses, the proportion of sperm exhibiting A and B category motility were summed and provided an estimate of progressive motile sperm (WHO, 1999). Sperm concentration (number of sperm  $\times 10^6/\text{mL}$  semen) was determined following dilution in fixation medium, by counting sperm present in  $5 \times 1\text{mm}^2$  cells in each of two chambers of a Neubauer haemocytometer, at 400x magnification. The count from each of the two chambers was averaged to provide a measure of sperm concentration. To assess morphology, smears were prepared from a 5 $\mu$ L drop of semen. These were left to air dry and stained using

the Diff-Quik stain (Baxter Diagnostics, Inc., McGraw Park, Illinois, USA). Two-hundred sperm cells were examined under oil immersion at 1000x magnification, and categorized as “normal” or “abnormal”, according to WHO (1999) guidelines. The percent sperm with normal morphology was used in subsequent analyses.

#### 5.3.5 DATA REDUCTION AND STATISTICAL ANALYSES.

All data were tested for normality with the Shapiro-Wilks normality test and transformed where necessary (face and body attractiveness ratings from Set 1 female raters were log transformed, and sperm motility was arcsin square root transformed). Note that while 118 males participated, the maximum  $N$  in this study is 116. Data were missing for some of the variables, due in particular to participants failing to complete the lifestyle questionnaire fully, and also to equipment failure when semen samples were delivered to the laboratory. As a consequence of these empty cells in the data files there is some minor variation in  $N$  (ranging from 101-116), dependent on which variables were used in each statistical analysis. Additionally, data from one male participant were excluded from all analyses due to an abnormally high sperm concentration ( $626 \times 10^6$  sperm/mL). All analyses for this study were performed using SPSS 13 for Mac OSX.

To reduce face and body ratings to a single overall appearance component for each phenotypic variable, separate principal component analyses (PCA) were performed to combine face and body ratings of attractiveness, masculinity, symmetry and averageness, respectively (Table 1). The four resulting appearance principal component scores (PCs) were used in subsequent analyses.

Following Soler et al. (2003) we also conducted a PCA that incorporated all three semen quality parameters (sperm motility, morphology, and concentration) into a single measure, which is the score on the first principal component that we refer to as the Sperm Index (eigenvalue = 1.35; variance explained = 45.1%; eigenvector motility = 0.60, morphology = 0.63, concentration = 0.50).

Semen quality is highly sensitive to environmental and lifestyle factors (Aitken et al., 2004). To control for factors associated with lifestyle, we ran general linear models with each semen quality parameter as the dependent variable and lifestyle factors entered as independent variables. We also entered testes size, and the potentially important procedural variables, time to produce the semen sample, time since previous ejaculation, and time from ejaculation to semen analysis, as independent variables. Each non-significant variable was removed by step-wise deletion, and the model was re-

run at each step until only significant variables remained. Significant models were obtained for sperm concentration and the Sperm Index, but no significant lifestyle or procedural factors were associated with sperm motility or morphology in our sample. For sperm concentration, variables remaining in the final model ( $F_{5,90}=7.16, p<0.001$ ) were time since last ejaculation ( $F_{1,90}=8.97, p<0.01$ ), exposure to toxins (eg. lead, pesticides, organic solvents) ( $F_{1,90}=7.18, p<0.01$ ), use of antibiotics and/or medication ( $F_{1,90}=4.86, p=0.03$ ), exposure to heat (including fever, wearing tight underwear, and regular exposure to a heated environment) ( $F_{1,90}=8.82, p<0.01$ ), and time taken to produce the ejaculate ( $F_{1,90}=3.99, p<0.05$ ). The only significant variable remaining for the Sperm Index model was amount of sexual activity per week ( $F_{1,100}=8.25, p<0.005$ ). The residuals from each of these significant final models were used for subsequent analyses of sperm concentration and Sperm Index.

#### 5.4 RESULTS.

Descriptive statistics for each of the semen quality parameters are shown in Table 2. Each of the mean values obtained from this sample of males was above the minimum criteria for normal semen as outlined by WHO (1999) (Motility > 50% sperm with forward progression; Morphology > 15% normal forms; Concentration >  $20 \times 10^6$  sperm/mL). Screening analyses revealed very high correlations between the three sets of attractiveness ratings (Set one females, Set two females, low fertility and Set two females, high fertility) (Table 3). Attractiveness was also significantly correlated with masculinity and symmetry but not with averageness (Table 3). We note that averageness may not have been attractive in this sample because of a low inter-rater agreement for these ratings. Analyses of averageness scores have nevertheless been included for completeness.

Attractiveness ratings from both sets of female raters were not correlated with semen quality parameters in this sample, even when females rated males at the fertile point of the menstrual cycle (Table 4). Furthermore, there were no significant correlations between semen quality parameters and any of the attractive traits (masculinity, symmetry, or averageness) (Table 5).

Our sample contained 44 men who had one or more semen parameters that fell below the minimum WHO criteria for normal semen. These men did not differ in appearance variables from the 72 men with normal semen parameters (attractiveness:  $t_{114}=0.550, p=0.583$ ; masculinity:  $t_{114}=1.057, p=0.293$ ; symmetry:  $t_{114}=-1.069, p=0.287$ ;

averageness:  $t_{114} = -1.131, p = 0.0261$ ).

The use of raw semen quality data (without controlling for lifestyle factors) or separate face and body ratings (rather than the combined face/body PCs) in our analyses made no qualitative or quantitative differences to the results.

## **5.5 DISCUSSION.**

Using a large sample of Australian men, we found no associations between attractiveness and semen quality, even when women rated attractiveness at the fertile point of their menstrual cycle, when male fertility might be expected to be of greatest importance. Furthermore, no relationship was found between semen quality and masculinity, symmetry, or averageness. Insofar as attractiveness indicates mate quality, our study suggests that visual attractiveness does not provide women with cues to male reproductive potential.

Our data do not support the findings of Soler et al. (2003). The importance of replication, even when methods differ, has been clearly demonstrated by studies examining the relationship between attractiveness and health (see Weeden & Sabini, 2005 for a review). There are strong arguments that attractiveness is a certificate of health (Grammer et al., 2003; Weeden & Sabini, 2005), and certainly attractiveness is correlated with rater perceptions of health (Kalick et al., 1998; Jones et al., 2001; Henderson & Anglin, 2003; Rhodes et al., 2003). However, studies investigating the correlation between attractiveness and actual health yield mixed results, particularly for males (Weeden & Sabini, 2005). For example Henderson & Anglin (2003) and Shackelford & Larsen (1999) found significant, positive correlations for men, while those by Hume & Montgomerie (2001) and Kalick et al. (1998) found no correlations. Consequently, evolutionary biologists exercise caution when making assumptions about health benefits of an attractive mate. Though of significant value, attempts to replicate studies in ecology and evolution are generally lacking (Palmer, 2000).

There are a number of key differences between our study and that of Soler et al. (2003) that could account for the different findings. Firstly, our ratings were on a seven-point scale as opposed to the 10-point scale used by Soler et al. (2003). While a seven-point scale may reduce the variance of ratings, variance in ratings collected using a seven-point scale has been sufficient to produce significant correlations with other attractive traits, and with sexual behaviour (see Rhodes et al., 2005). Secondly, Soler et al. (2003) studied only faces. We have improved on this by including bodies as well in

our analyses, because both faces and bodies are important when making mate choice decisions (Peters et al., 2007). Incorporation of body appearance improves the biological relevance of our study. Thirdly, the determination of ovulation differs between the two studies: Soler et al. (2003) estimated ovulation using self-reported cycle-lengths, and approximated fertility based on the probability of conception following sex on the day of testing. However self-reported menstrual cycle length is prone to very high measurement error (Small et al., 2007). We therefore used ovulation predictor kits to confirm if and when ovulation occurred, which provided a more accurate and precise method of determining ovulation.

While raw mean data for each of the semen quality variables collected during this study closely resemble those described in Soler (2003), suggesting that our semen measurements are typical of an adult male population, our study did not reproduce the correlations found between attractiveness and semen quality parameters. In their study of 66 men, Soler et al. (2003) found significant correlations of approximately 0.3 between attractiveness and sperm motility, morphology, and sperm index, but no correlation between attractiveness and sperm concentration. In a second experiment, Soler et al. chose a subsample of 12 men and classed them into groups of high, normal and low semen quality comprising 4 individuals per group. With this limited sample, they found higher correlations of around 0.6 between attractiveness and all semen quality parameters except sperm concentration. The semen quality of Soler et al.'s low group was considerably lower than the WHO criteria for normal semen, and it could be argued that their significant associations between attractiveness and semen quality could be due to the inclusion of these infertile men. However, our studies were based on a comparatively large sample of 118 men: a sample size that is greater than that of a number of other studies investigating phenotypic cues to semen quality (e.g Firman et al., 2003,  $N=50$ ; Manning et al., 1998,  $N=61$ ; Soler et al. 2003,  $N=66$ ). Importantly, our sample included 44 men with one or more semen traits that would be classified as below normal by WHO standards. The attractiveness of these men did not differ from that of men with normal or above normal semen quality.

While our results suggest that females are not sensitive to visual cues to semen quality that are available in a static photograph, other studies suggest that male fertility is nonetheless reflected phenotypically via measured body fluctuating asymmetry (FA) (Manning et al., 1998; Firman et al., 2003). Both Manning et al. (1998) and Firman et al. (2003) found significant negative relationships between FA and semen quality

parameters. Using ratings of symmetry, rather than measurements, the current study did not find a relationship between (a)symmetry and semen quality. It may be that measurement represents a more sensitive method for assessing the subtle phenotypic expression of traits that correlate with semen quality. Studies of face perception show that humans are finely attuned to the accurate detection of FA in faces (Simmons et al., 2004b), although the same may not be true for bodies (Rhodes & Simmons, 2007). Our data suggest that even if body asymmetry does correlate with semen quality in humans, women may be unable to accurately perceive these phenotype-linked cues to fertility.

Several studies suggest that olfactory cues may be important in signaling mate quality. Body odour provides cues to genes associated with immune function (the major histocompatibility complex, MHC), such that women are attracted to the smell of men with genes dissimilar to their own at the MHC (Wedekind & Furi, 1997). Furthermore, women show a preference for the scent of men with relatively low body asymmetry, particularly at the fertile point of the menstrual cycle, when conception is most likely (Thornhill et al., 2003). Therefore, given the important cues to mate quality that can be conveyed through body odour, research incorporating olfactory cues may be useful to further investigate whether females are sensitive to signals of male fertility.

Determining biological markers of mate quality that are signaled by attractiveness in humans is a challenging task, particularly because of individual differences in grooming and lifestyle habits. Despite controlling for these variables, this study found no evidence that physically attractive males provide females with reproductive benefits via increased semen quality. Therefore, the phenotype-linked fertility hypothesis does not seem to be generally applicable to human mate choice.

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Table 1. Principal component analyses combining ratings of appearance variables for faces and bodies. Separate PCAs were performed for each appearance variable.

	Attractiveness <sup>†</sup>	Attractiveness LF <sup>§</sup>	Attractiveness HF <sup>§</sup>	Masculinity	Symmetry	Averageness
Eigenvalue	1.49	1.47	1.44	1.47	1.16	1.08
Percent	74.50	73.64	72.10	73.4	57.84	53.77
Eigenvectors						
Face	0.71	0.86	0.85	0.71	0.71	0.71
Body	0.71	0.86	0.85	0.71	0.71	0.71

<sup>†</sup> Female raters from Set 1

<sup>§</sup> Female raters from Set 2, LF = Low fertility ratings, HF = High fertility ratings

Table 2. Average values ( $\pm$  S.D.) for semen quality variables<sup>^</sup>.

Semen Quality Parameter	Mean ( $\pm$ S.D.)	<i>N</i>
Motility	62.4 ( $\pm$ 16.8)	105
Morphology	35.0 ( $\pm$ 8.2)	113
Concentration	90.7 ( $\pm$ 62.2)	108
Sperm Index	0.0 ( $\pm$ 1.1)	102

<sup>^</sup>Semen quality was analysed according to WHO (1999) criteria.

Motility = percentage of sperm with forward progression.

Morphology = percentage sperm with normal forms.

Concentration = number of sperm  $\times 10^6$ /mL semen.

Table 3. Zero order correlations between overall attractiveness ratings, and ratings of components of attractiveness, symmetry, masculinity, and averageness.

	Attractiveness <sup>†</sup>	Attractiveness LF <sup>§</sup>	Attractiveness HF <sup>§</sup>	Masculinity	Symmetry
Attractiveness <sup>†</sup>	1				
Attractiveness LF <sup>§</sup>	0.926***	1			
Attractiveness HF <sup>§</sup>	0.927***	0.960***	1		
Masculinity	0.668***	0.716***	0.703***	1	
Symmetry	0.479***	0.457***	0.440***	0.407***	1
Averageness	-0.074	-0.038	-0.069	0.032	-0.083

\*\*\* $P < 0.001$

<sup>†</sup> Female raters from Set 1

<sup>§</sup> Female raters from Set 2, LF = Low fertility ratings, HF = High fertility ratings  
 $N=116$ . Note some individuals had missing cells for semen data, making  $N < 116$  for analyses of semen parameters (See Table 2 for values of  $N$ ).

Table 4. Zero order correlations between attractiveness and semen quality variables. Attractiveness ratings are by two independent sets of females.

	Females - Set 1	Females - Set 2	
		Low fertility	High fertility
Motility (N=104)	0.035	-0.052	-0.020
Morphology (N=112)	0.001	-0.091	-0.058
Concentration (N=107)	-0.053	-0.054	-0.075
Sperm Index (N=101)	-0.007	-0.029	-0.026

Table 5. Zero order correlations between attractive traits and semen quality variables.

	Masculinity	Symmetry	Averageness
Motility (N=104)	0.026	-0.121	-0.111
Morphology (N=112)	0.033	-0.075	-0.045
Concentration (N=107)	-0.084	-0.061	0.062
Sperm Index (N=101)	0.012	-0.137	-0.034

## **CHAPTER SIX**

### **GENERAL DISCUSSION.**

## **CHAPTER SIX: GENERAL DISCUSSION.**

The main objectives of this thesis were to investigate whether male faces and bodies convey signals of mate quality, and whether female preferences for such signals are adaptations for obtaining immediate and/or genetic benefits for offspring. These aims were addressed through a series of studies that investigated female preferences for male faces and bodies, and used semen quality and testosterone (T) as indicators of mate quality.

### **6.1 PREFERENCES FOR MALE SECONDARY SEXUAL CHARACTERISTICS.**

In this thesis, I aimed to determine whether faces and bodies each provide cues that may be important in human mate choice. I also aimed to show that there is no interaction between face and body attractiveness in order to validate the widespread methodology of studying faces and bodies separately in human studies of mate choice. Chapter 2 showed that rated face and body attractiveness each make independent contributions to overall attractiveness, with no interaction. These results confirm that the use of separate faces and bodies in the context of mate choice is a valid approach. To the extent that perceptions of attractiveness influence mate choice (see Rhodes et al., 2005), both face and body attractiveness are likely to drive mating decisions in natural situations. Thus, although mate choice studies that are based on only face or body attractiveness will yield biologically significant results, they would be improved by including both elements.

Prior studies have found evidence for increased preferences for masculinity and symmetry at the fertile point of the menstrual cycle, using methods that require women to choose between subtle variations in computer-generated stimuli, which may not capture functional female responses that influence mate-choice (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Little et al., 2007a; Little et al., 2007b). In Chapter 3, I aimed to generalise these findings to a more biologically relevant context by using real photographs of men, and to determine whether cyclic changes reflect increased preferences for a superior quality mate when conception is likely. Although there is strong evidence from studies using artificial stimuli for increased masculinity preferences when the chance of conception is high (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Little et al., 2007a),

my research suggests that the menstrual cycle shift may be too subtle to affect preferences for real faces and bodies. Furthermore, my menstrual cycle study found no evidence for a shift in face and body symmetry preferences. These results suggest that menstrual cycle shifts detected from responses to different variations of the same computer-generated male image, may be too subtle to influence responses to real faces and bodies, and raise doubts about the biological relevance of previous findings.

## **6.2 DO MALE SECONDARY SEXUAL CHARACTERISTICS SIGNAL MATE QUALITY?**

Chapters 2 and 3 showed that male secondary sexual traits, and symmetric features are attractive in male faces and bodies at both high and low fertility phases of the menstrual cycle. A female preference for male secondary sexual traits has been hypothesised to be an adaptation for gaining high quality mates. Specifically, male secondary sexual characteristics are proposed to reflect parasite resistance (Hamilton & Zuk, 1982), and honestly signal fertility status (Hillgarth et al., 1997), because of their dependence on testosterone (T) for development. Elevated testosterone levels during puberty stimulate the growth of secondary sexual traits and initiate the completion of spermatogenesis (see Hillgarth et al., 1997 for a review). However, T also suppresses the immune system, which can increase the risk of infections if an individual does not carry resistance to parasites, but can also reduce the production of antisperm antibodies (which can damage sperm) (Hillgarth et al., 1997), and increase fertility (Lehmann & Muller, 1986). Therefore the expression of T-dependent secondary sexual traits in males may provide choosy females with honest signals of both parasite resistance (Hamilton & Zuk, 1982; Folstad & Karter, 1992) and fertility status (Hillgarth et al., 1997).

In this thesis, I aimed to determine whether secondary sexual traits honestly signal T levels, and whether females show a preference for males with high T (Chapter 4). I found no significant correlations between T levels and perceived attractiveness or masculinity, which suggests that women are not sensitive to any physical cues (at least those present in a photograph of the face and body) that may signal current T levels.

Although I found no evidence that secondary sexual characteristics signalled T, I did find evidence that T itself may be under sexual selection, because it was correlated with mating success (Chapter 4). Females may gain indirect genetic benefits for offspring from a high T mate, because baseline T levels are heritable (Meikle et al., 1988). My research has shown that females do not appear to be sensitive to physical

cues to T in male faces and bodies, so an increase in mating success for high T males could potentially be behaviourally mediated via increased male mating effort, or a female attraction to male behavioural displays.

I also examined directly the hypothesis that the expression of T-dependent secondary sexual traits in males provides females with honest signals of fertility status but found no significant correlation between rated masculinity and semen quality (Chapter 5). Although females show a preference for masculine males, my studies suggest that females do not gain any reliable information about semen quality from the expression of male secondary sexual characteristics. Symmetry and averageness are also proposed to signal mate quality (Thornhill & Gangestad, 1999), however this study found no evidence that either of these traits was associated with semen quality. I also examined whether females show an increased visual preference for males with superior semen quality during the high fertility phase of the menstrual cycle. Theoretically, this would have improved a female's ability to secure 'good genes' for their offspring. However, I found no evidence for any associations between attractiveness and semen quality, irrespective of when during the cycle preferences were tested (Chapter 5). These results suggest that women are not sensitive to any cues to male fertility that may be present in static images of the male face and body. Furthermore, it is unlikely that physically attractive males provide females with direct reproductive benefits via increased semen quality.

In summary, the findings of this thesis suggest that both the face and the body are important for human mate preferences, but that they provide little information about putative aspects of 'quality' specific to semen quality or T, despite the proposed importance of male secondary sexual traits for honestly signalling information about mate quality. Although secondary sexual characteristics do not appear to signal fertility status or T levels, they are still rated as attractive by females, and males who display these traits have higher mating success (Chapter 4, and see Rhodes et al., 2005). This preference suggests that the expression of secondary sexual traits is under current sexual selection, even though they do not appear to confer T-related benefits. It is possible that females show innate preferences that might have been ancestrally adaptive, prior to the introduction of modern medicine, which may interfere with honest signalling of mate quality. Alternatively, secondary sexual characteristics may signal other aspects of mate quality, not examined in this thesis. Further investigations of mate quality signalling in human faces and bodies might examine other aspects of quality, for

example, measures of health, and/or genetic diversity within the Major Histocompatibility Complex, which is associated with immune function (Doherty & Zinkernagel, 1975; Carrington et al., 1999). Future studies should attempt to maximise the biological relevance of any methodologies, if implications for actual mate choice are to be drawn from experimental results.

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