Social Perception of Facial cues of Adiposity

Claire Fisher

Submitted in fulfillment of the requirements for the Degree of Doctor of Philosophy

School of Psychology
College of Science and Engineering
University of Glasgow

July 2017

General Abstract

Previous research suggests that facial characteristics associated with body mass index (BMI) play an important role in health and attractiveness judgments of faces. However, very little work has investigated the factors that predict individual differences in preferences for facial cues of adiposity or how these individual differences are related to social outcomes.

In light of the above, the first two empirical chapters of this thesis investigated the relationships between individual differences in preferences for facial cues of adiposity and (1) the BMI of men's and women's actual romantic partners and (2) disgust sensitivity. Analyses suggested that people with particularly strong preferences for slim-looking faces were more likely to have partners with low BMI and that men, but not women, who scored higher on pathogen disgust showed stronger aversions to faces displaying cues associated with high BMI.

The third chapter investigated how people integrate information from shape cues of adiposity and information from skin color when judging the health and attractiveness of faces. Analyses showed that preferences for cues of low BMI were particularly strong when assessing faces displaying skin color cues associated with the absence of illness. These results suggest that integrating information from shape cues of adiposity and information from skin color could allow people to distinguish between individuals with low BMI because they are healthy and those with low BMI due to illness.

Most research investigating the role of facial cues of adiposity in social perception has focused on the possible role of facial adiposity as a health cue. However, it is also possible that facial cues of adiposity contain other types of information, such as information about a person's reported sociosexual orientation (openness to short-term, uncommitted sexual relationships). To explore this issue, the fourth empirical chapter of my thesis investigated the relationship between facial correlates of BMI and women's sociosexual orientation. Although analyses suggested that slimmer women reported greater openness to short-term, uncommitted sexual relationships, the observed relationships were weak and, thus, unlikely to play an important role in social interactions.

Together these studies support the claim that responses to facial cues of adiposity are related to romantic partner choice and function to distinguish between healthy and unhealthy individuals.

Table of Contents

Page 2. **General Abstract**

Page 5. **List of Tables**

Page 6. **List of Figures**

Page 7. **Publication Statement**

Page 8. **Acknowledgments**

Page 9. **Author's Declaration**

Page 10. **Chapter 1: Introduction**

Page 44. **Chapter 2: Do assortative preferences contribute to assortative mating for adiposity?**

Page 64. **Chapter 3: Individual differences in pathogen disgust predict men's, but not women's, preferences for facial cues of weight**

Page 76. **Chapter 4: Integrating shape cues of adiposity and color information when judging facial health and attractiveness**

Page 93. **Chapter 5: Is women's sociosexual orientation related to their physical attractiveness?**

Page 106. **Chapter 6: General Discussion**

Page 125. **Conclusion**

Page 126. **References**

List of Tables

Page 56. **Table 1.** Correlations among men’s BMI, women’s BMI, men’s preferences for cues of BMI in women’s faces, and women’s preferences for cues of BMI in men’s faces.

Page 102. **Table 2.** Correlations between aspects of sociosexual orientation (assessed using Penke and Asendorpf’s SOI-R) and aspects of women’s physical attractiveness. Spearman’s rho (and p values) are reported.

List of Figures

Page 80. **Figure 1.** An example of a composite female face that has been manipulated to possess all possible combinations of the factors *color dimension* (red, yellow), *color value* (increased, decreased), and *facial adiposity* (increased, decreased).

Page 86. **Figure 2.** The significant interaction between *facial adiposity* and *color value*. The effect of adiposity was greater when rating faces with increased color values than when rating faces with decreased color values. Bars show means and SEM.

Page 102. **Figure 3**. The relationship between global SOI-R scores and scores on the attractiveness component.

Publication Statement

Parts of this thesis have been published in the following journal articles:

Fisher, C. I., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2016). Is women's sociosexual orientation related to their physical attractiveness? *Personality and Individual Differences*, *101*, 396-399.

Fisher, C. I., Fincher, C. L., Hahn, A. C., Little, A. C., DeBruine, L. M., & Jones, B. C. (2014). Do assortative preferences contribute to assortative mating for adiposity? *British Journal of Psychology*, *105*, 474-485.

Fisher, C. I., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2014). Integrating shape cues of adiposity and color information when judging facial health and attractiveness. *Perception*, *43*, 499-508.

Fisher, C. I., Fincher, C. L., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2013). Individual differences in pathogen disgust predict men's, but not women's, preferences for facial cues of weight. *Personality and Individual Differences*, *55*, 860-863.

Acknowledgements

I feel incredibly grateful for the solid support network I have been fortunate enough to have over the past 5 years. I could not have accomplished this without all of you behind me.

Firstly, I would like to thank Ben Jones and Lisa DeBruine for their excellent mentorship. I cannot thank you enough for your guidance, generosity, and support. You are the academic dream team! I would like to extend my gratitude to everyone who has been part of the Facelab at some point during my PhD. People have come and gone, but all of you have contributed to making this an unforgettable experience full of fond memories. I would like to give Amanda Hahn a big shout out for all of her helpfulness and laughter.

Special recognition goes out to my friends and family for their endless encouragement and support. Thank you for being there through the highs and lows. All of you have inspired me more than you will ever know.

Author's Declaration

I, Claire Fisher, hereby declare that this thesis has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged.

Date: 3rd May 2017 Signature: [redacted]

Chapter 1: Introduction

How does facial attractiveness influence behaviour?

The human face and the remarkable face processing abilities of humans have been sources of great interest within the fields of philosophy, psychology, and science for centuries. For many years, researchers from these fields generally shared the view that facial attractiveness is determined by arbitrary cultural conventions (Berry, 2000; Etcoff, 1999). This view was even endorsed by Darwin based on his observations of large cultural differences in beautification practices (Darwin, 1871). While there is indeed evidence for social transmission of face preferences and cultural influences on facial attractiveness judgments (see Little et al., 2011a for a review), several studies have reported cross-cultural agreement regarding which faces are attractive (Langlois, 2000; Perrett, 1998; Rhodes et al., 2001; but see also Jones & Hill, 1993 for weaker agreement). Other work suggests that some aspects of face preferences emerge early in development prior to assimilation of cultural standards of beauty (Geldart et al., 1999; Rubenstein et al., 1999; Samuels et al., 1994; Slater et al., 1998, 2000). Consequently, many researchers have attempted to establish what makes a face universally attractive.

It has been argued that attractiveness cannot be reduced to a single principle (e.g., mathematically harmonious proportions; Armstrong, 2004). Instead, facial attractiveness appears to be determined by the interplay of a multitude of components, such as averageness, skin coloration, symmetry, sexual dimorphism, demeanour, youthfulness, and grooming behaviours (Berry, 2000; Cunningham, 1986; Etcoff, 1999; Little et al., 2011b; Thornhill & Gangestad, 1999). Should the perceiver know the identity of a face, attractiveness may also be influenced by nonphysical characteristics (e.g., how much one likes the individual, Kniffin & Wilson, 2004).

Just as a person's likeability may influence perceptions of their attractiveness, research into the "what is beautiful is good" stereotype has shown that attractive faces elicit positive personality attributions (Dion et al., 1972; Eagly et al., 1991; Langlois et al., 2000). Moreover, attractive faces activate reward circuitry in the brain (Aharon et al., 2001; O'Doherty et al., 2003) and motivate sexual behavior and the formation of same-sex alliances (Berscheid & Walster, 1974; Feingold, 1990; Rhodes et al., 2005; Thornhill & Gangestad, 1999). In light of these findings, it is hardly surprising that facial attractiveness has important social outcomes in a variety of settings. In terms of employment-related outcomes, facially attractive people are more likely to succeed in mock interviews (Cash & Kilcullen, 1985), be hired for actual jobs (Chiu & Babcock, 2002; Marlowe et al., 1996), and earn higher salaries (Hamermesh & Biddle, 1994). Indeed, research points towards a link between facial attractiveness and upward economic mobility, particularly for women (Elder, 1969; Holmes & Hatch, 1938). Despite some evidence suggesting a decrease in workplace attractiveness biases at the turn of the 21st Century (Hosoda et al., 2003), findings from recent studies suggest that positive discrimination towards facially attractive individuals is an ongoing occurrence in the labor market (Berri et al., 2011; Fletcher, 2009; Mobius & Rosenblat, 2006).

In addition to achieving higher occupational success, evidence suggests that facially attractive individuals are also more successful in the political arena. Studies conducted in the laboratory and studies of real voting behavior yield similar results, whereby physically attractive candidates are more likely to be elected than relatively unattractive candidates (e.g., Banducci et al., 2008; Berggren et al., 2010; Budesheim & DePaola, 1994; Rosenberg et al., 1986). Although this phenomenon has typically been attributed to the halo effect (i.e., the automatic tendency for people to ascribe positive personality traits to attractive individuals; Dion et al., 1972), some researchers have suggested that preferences for facially attractive leaders are potentially related to disease-avoidance mechanisms (see e.g., White et al., 2013). Consistent with this explanation, White et al. (2013) found that experimentally priming concerns about infectious disease leads people to place particularly high importance on facial attractiveness in political candidates.

Alongside influencing electoral outcomes, facial attractiveness also appears to influence the social-decision making process behind economic outcomes. Research suggests that people are more willing to cooperate with facially attractive individuals than with relatively unattractive individuals (see Langlois et al., 2000, for a meta-analysis). This finding translates into the domain of economic games, with several studies reporting that people are more cooperative with, and generous towards, physically attractive partners (Andreoni & Petrie, 2008; Hancock & DeBruine, 2003; Solnick and Schweitzer, 1999). Similarly, Wilson and Eckel (2006) found that people expected attractive participants to be trustworthy when playing a trust game, resulting in greater placement of trust in attractive partners relative to unattractive partners. By contrast, studies using a prisoner's dilemma game have found that facial attractiveness is negatively related to young men's, but not women's or older men's, cooperative tendencies (Shinada & Yamagishi, 2014; Takahashi et al., 2006). Takahashi et al. (2006) suggested that, given physical attractiveness is a key determinant of reproductive success in short-term mating, less attractive men with lower short-term mating success may need to adopt an alternative mating strategy whereby increasing their cooperation allows them to accumulate resources.

Why might facial cues of health be important for attractiveness?

By forming affiliations with healthy social partners and selecting healthy mating partners, people maximise their reproductive success in a number of ways. For example, choosing to interact and mate with healthy rather than unhealthy individuals decreases the likelihood of contracting infectious illnesses (for oneself and offspring) and increases the likelihood that offspring will inherit pathogen-resistant genetic material (Zuk, 1992). Given the importance of health in maximising reproductive success, it has been suggested that phenotypic markers of good health are generally perceived as attractive (Rhodes et al., 2005). Consequently, many researchers have investigated whether facial attractiveness is related to perceptions and measures of health.

Is facial attractiveness related to physical health?

Evidence for correlations between facial attractiveness and health-related outcomes is mixed. Some studies have found that facially attractive individuals live for longer (Henderson & Anglin, 2003) and are less likely to suffer from chronic illnesses (Nedelec & Beaver, 2014). Shackelford and Larsen (1999) tested for an association between facial attractiveness and multiple health measures, such as cardiovascular health (assessed using cardiac recovery time following moderate exercise) and self-reported frequency of illness. Facially attractive men displayed greater cardiovascular health and reported lower frequency of sore throat or coughing symptoms relative to unattractive men. Facially attractive women reported lower frequency of headaches relative to unattractive women (Shackelford & Larsen, 1999), although this work has been criticised for running a relatively large number of comparisons without correcting for multiple tests (e.g., Rhodes et al., 2003a). Further strengthening the body of evidence suggesting that facial attractiveness is indeed linked to actual health, Hume and Montgomerie (2001) found that facial attractiveness was best predicted by past health problems in a relatively large sample of women (N = 94). However, facial attractiveness was not related to past health problems in this study's sample of men (N = 95).

While the above findings suggest that facial attractiveness is related to various measures of physical health, other studies have reported null results for a link between facial attractiveness and actual health (Kalick et al., 1998; Rhodes et al. 2003a; Thornhill & Gangestad, 2006). Kalick et al. (1998) investigated whether facial attractiveness during adolescence predicted health outcomes over the lifespan (adolescence, middle adulthood, or later adulthood). Despite being related to perceptions of health, adolescent facial attractiveness was not a significant predictor of health at any stage of the lifespan. Similarly, Thornhill and Gangestad (2006) found that facial attractiveness was unrelated to various health measures in a large sample of men (N= 203) and women (N=203).

While self-reported medical history was the main method of assessing the link between facial attractiveness and measures of health in the aforementioned studies, other researchers have investigated the link between facial attractiveness and objective measures of immune function. Heterozygosity in the major histocompatibility complex (MHC) is associated with immunocompetence; MHC genes encode proteins implicated in immune response (Mungall et al., 2003). Although it has been suggested that MHC heterozygosity is linked to facial attractiveness, evidence for such a link is equivocal. Roberts et al. (2005) found that the faces of MHC-heterozygous men were judged as healthier and more attractive than the faces of MHC-homozygous men. A more recent study, which assessed two measures of genetic diversity (individual mean heterozygosity and the genetic distance between alleles), also reported a significant positive relationship between MHC heterozygosity and facial attractiveness in men (Lie et al., 2008). MHC genetic diversity did not predict facial attractiveness in Lie et al.'s sample of women, however. Adding to the null findings, Coetzee et al. (2007) found that MHC heterozygosity was unrelated to facial attractiveness in a sample of women and Thornhill et al. (2003) found that MHC heterozygosity was unrelated to facial attractiveness in both sexes. Together, the above findings suggest that facial attractiveness may be a more reliable cue to men's genetic quality than it is to women's.

In addition to genetic quality, facial attractiveness has been linked to direct measures of imunnocompetence in men, such as immune response to vaccinations. Rantala et al. (2012, 2013a) assessed men's antibody response one month after a dose of hepatitis B vaccine. Facially attractive men showed stronger immune responses to the hepatitis B vaccination than men judged as less attractive. Furthermore, this positive relationship between facial attractiveness and antibody response was moderated by cortisol (Rantala et al., 2012), a glucocorticoid stress hormone that plays an important role in regulating the immune system (see e.g., Sapolsky, 2000 for a comprehensive review). Since immunosuppression is associated with prolonged elevation of glucocorticoid levels (see Sapolsky, 2000), it has been suggested that high trait (i.e., average) cortisol levels may be a biomarker for poor health. Some research has demonstrated that men with lower average cortisol, and consequently greater immunocompetence, have more attractive faces than men with higher average cortisol (Moore et al., 2011a, 2011b). The link between cortisol and facial attractiveness may be complex, however, with some studies finding that the relationship is modulated by testosterone level (Moore et al., 2011a; Rantala et al., 2012).

While these results strengthen the evidence suggesting that immunocompetence is associated with facial attractiveness in men (Lie et al., 2008; Rantala et al., 2012, 2013a; Roberts et al., 2005), there is limited evidence for an association between immunocompetence and facial attractiveness in women. Although Rantala et al. (2013b) reported that lower average cortisol was associated with higher attractiveness ratings of women's faces, facial attractiveness did not predict immune responsiveness to a hepatitis B vaccination in this sample of women. Contrary to the significant negative relationship between women's cortisol and facial attractiveness reported by Rantala et al. (2013b), other recent studies have observed no significant correlations between women's average salivary cortisol and ratings of their facial attractiveness (Han et al., 2016; Gonzalez-Santoyo et al., 2015), suggesting that Rantala et al.'s (2013b) finding may not be robust.

While the findings described above are for the possible relationship between facial attractiveness and measures of health, other work has examined possible links between health and other aspects of facial appearance, such as symmetry, averageness, secondary sexual characteristics, adiposity, and skin coloration.

Is facial symmetry related to attractiveness and health?

Variation exists across individuals in their ability to maintain developmental stability in spite of environmental and genetic stressors, such as pathogen load and mutation rate, respectively (Møller, 1997). Developmental 'noise' can result in fluctuating asymmetry (phenotypic differences between the right and left sides of affected individuals) above and beyond biologically normal asymmetry (Jones & Hill, 1993). Because bilateral symmetry is a phenotypic manifestation of optimal developmental stability, this trait has been proposed to be an indicator of genetic quality. Some researchers have also put facial symmetry forward as an index to prior health given that an individual's ability to resist asymmetric growth is dependent on environmental factors, such as nutrient intake and parasite load (Gangestad & Buss, 1993; Møller, 1997). Consequently, preferences for symmetrical faces may provide perceivers with both direct (e.g., contagion avoidance) and indirect (e.g., healthy genes for offspring) benefits.

Early work investigating the link between facial symmetry and attractiveness typically used ‘chimeric’ face images created by vertically bisecting a face and then aligning the half-face with its mirror reflection (producing two chimeras for each face). Studies using this method of image manipulation reported stronger preferences for original asymmetric faces than for perfectly symmetric chimeric versions of the same faces (Kowner, 1996; Langlois et al., 1994). However, it has since been established that chimeric manipulations introduce structural abnormalities into symmetric faces that will likely lower attractiveness (see Perrett et al., 1999). Studies employing a more methodologically sound symmetry manipulation have reported positive relationships between facial symmetry and rated attractiveness (Perrett et al., 1999; Rhodes et al., 1998). Preferences for symmetry using manipulated face images have been reported in Western (Little & Jones, 2003, 2006) and Eastern (Rhodes et al., 2001) samples, as well as in African hunter-gatherers (Little et al., 2007).

Further evidence that facial symmetry is perceived as attractive comes from several studies measuring naturally occurring asymmetries in face images. Naturally symmetric faces receive higher attractiveness ratings than relatively asymmetric faces (Grammer & Thornhill, 1994; Jones & Hill, 1993; Penton-Voak et al., 2001; Perrett et al., 1999; Scheib et al., 1999). Moreover, in a study examining symmetry differences between pairs of monozygotic twins (who are genetically identical, but differ developmentally), the more facially symmetric twin received higher attractiveness ratings (Mealey et al., 1999). Together, findings from studies examining symmetry preferences in both manipulated and unmanipulated face images demonstrate that symmetry has a positive effect on attractiveness judgments. These findings are complemented by studies reporting a positive relationship between facial symmetry and perceptions of health (Fink et al., 2006a; Jones et al., 2001, 2004; Rhodes et al., 2007), suggesting that symmetry plays an equally important role in health judgments.

Although the evidence linking facial symmetry to judgments of health and attractiveness is relatively compelling, evidence for a link between facial symmetry and actual health is far more mixed. Thornhill and Gangestad (2006) found that facial symmetry predicted the number of respiratory infections experienced over the previous three years, whereby individuals displaying greater facial symmetry reported a lower incidence of colds and flu. While facial symmetry also predicted reduced frequency of antibiotic use, albeit at a marginal level of significance, it was unrelated to stomach infections in this sample (Thornhill & Gangestad, 2006). However, the largest study investigating the relationship between symmetry and actual health to date (N=4732), Pound et al. (2014) observed no significant association between facial symmetry and longitudinal measures of childhood health (such as proportion of childhood years spent unwell and total number of infections). Pound et al.'s (2014) null result in this large sample suggests that, despite being reliably associated with perceptions of health and attractiveness, facial symmetry may not be a reliable biomarker for health.

Is facial averageness related to attractiveness and health?

Facial averageness describes proximity to a spatially average face within a population. As with facial symmetry, deviations from facial averageness can result from genetic and environmental stressors (Thornhill & Møller, 1997). Consequently, average faces may reflect genetic diversity and good resistance to pathogens that would otherwise impede an individual's developmental stability (Gangestad & Buss, 1993; Thornhill & Gangestad, 1993). Given that faces displaying mathematically average trait values signal genetic diversity, some researchers have proposed that average faces are more attractive (Mitton & Grant, 1984; Thornhill & Gangestad, 1993). Indeed, MHC heterozygosity (i.e., genetic diversity) is positively related to facial attractiveness (Roberts et al., 2005) and facial averageness (Lie et al., 2008) in some studies (but see Coetzee et al., 2007).

The notion that average faces are more attractive has existed since the Nineteenth Century when Galton (1878) found that blending multiple faces together produced a more attractive face than the constituent faces. More recently, researchers have improved on these techniques by creating digitally blended composite faces that average the shape, color and texture information from multiple face images. Generally, the higher the number of images in a composite image, the higher the attractiveness rating it is awarded (Langlois & Roggman, 1990; Langlois et al., 1994). This pattern of results holds in Western

(Jones et al., 2007a), Eastern (Rhodes et al., 2001), and hunter-gatherer (Apicella et al., 2007) populations. Furthermore, researchers have observed the same pattern of results even when controlling for facial symmetry (Apicella et al., 2007; Jones et al., 2007a), a potential confound given that average faces tend to be more symmetric and symmetry is associated with attractiveness. Jones et al. (2007a) demonstrated that preferences for facial averageness remained strong regardless of whether the effects of symmetry were controlled or uncontrolled for, suggesting that symmetry has little bearing on attractiveness judgments of average faces.

Several researchers have identified skin color/texture as another potential confound in studies examining the link between facial averageness and attractiveness. In early composite studies (e.g., Langlois & Roggman, 1990), increasing the number of images blended together simultaneously increased the smoothness of skin texture. Alley and Cunningham (1991) noted the averaging of skin imperfections and blemishes using this method could bias attractiveness judgments. As a result, many subsequent studies controlled for this potential confound by standardizing the skin color/texture of faces used to generate composite images and all of these studies reported a positive association between averageness and attractiveness (Apicella et al., 2007; Jones et al., 2007a).

Although facial averageness is perceived as healthy (Rhodes et al., 2001, 2007), evidence that this trait is linked to actual health is mixed. Rhodes et al. (2001) found that childhood health in men and current health in women were both predicted by averageness. A subsequent study reported that faces below median averageness were driving this relationship, however (Zebrowitz & Rhodes, 2004). MHC heterozygosity has been shown to predict facial averageness in men, but not in women (Lie et al., 2008). Given that there is some evidence linking MHC heterozygosity to superior immune functioning in humans (Thursz et al., 1997; Carrington et al., 1999), Lie et al.'s (2008) finding could be interpreted as demonstrating a link between facial averageness and actual health, at least in men.

Are secondary sexual characteristics related to attractiveness and health?

On average, there are structural differences between male and female faces. Men tend to have larger jawbones, deeper set eyes, and thinner lips than women (Penton-Voak et al., 2001). These face shape differences are caused, in part, by the sex hormones at play during adolescence, such as the ratio of testosterone to estrogen (Bardin & Catterall, 1981; Enlow, 1990). Higher testosterone promotes facial bone growth in men until the early 20s, whereas estrogen caps facial bone growth in women whilst also enhancing lip fullness (Thornhill & Gangestad, 1993; Thornhill & Grammer, 1999).

Many researchers have suggested that exaggerated secondary sexual characteristics (femininity in women and masculinity in men) should be attractive because they signal information about the genetic quality of an individual. Indeed, there is convincing evidence that femininity in female faces is perceived as attractive. Cunningham (1986) measured the femininity of women's facial features and found that feminine features were positively related to attractiveness, a finding that was later replicated in various cultures (Jones & Hill, 1993). More recently, studies objectively manipulating sex-typicality in composite face images (i.e., to display more/less exaggerated feminine characteristics) found that more feminine female faces were awarded higher attractiveness ratings (Fraccaro et al., 2010; Perrett et al., 1998; Welling et al., 2008).

In men, the link between sexually dimorphic face shape and attractiveness is less straightforward. Some studies using facial measurements to quantify masculinity in male faces have shown that women prefer large jaws (Cunningham et al., 1990; Grammer & Thornhill, 1994), a 'masculine' feature reliably associated with dominance ratings of men's faces (Berry & Brownlow, 1989; McArthur & Berry, 1987). More recently, and relatedly, Boothroyd et al. (2013) found that rated and morphometric masculinity both correlated positively with attractiveness in men's faces. Furthermore, some studies assessing preferences for objectively manipulated sex-typicality in composite face images have found that women tend to prefer masculinized rather than feminized male faces (DeBruine et al., 2006; Johnston et al., 2001).

In contrast to these findings showing preferences for *masculinity* in men's faces, several studies have reported preferences for more *feminine* characteristics in men's faces (Little & Hancock, 2002; Perrett et al., 1998; Rhodes et al., 2000). Perrett et al. (1998) presented Caucasian and Japanese participants with masculinized and feminized versions of male faces belonging to both ethnicities. Participants from both cultures exhibited a stronger preference for femininity in men's faces and this pattern of results was consistent regardless of stimuli/participant ethnicity (Perrett et al., 1998). Although some researchers have suggested that these inconsistent results for the effects of sexually dimorphic shape cues on men's facial attractiveness are due to methodological issues (Rennels & Langlois, 2008), this does not appear to be the case (DeBruine et al., 2006, 2010). Inconsistencies in results for the effects of sexually dimorphic shape cues on men's facial attractiveness across studies may be due to individual differences in women's preferences for masculine men, such as those related to women's own condition, market value, or hormonal profile (for a review see Little et al., 2011b). Researchers have recently proposed that these individual differences may not be robust, however (Scott et al., 2012).

In comparison with the mixed findings for a link between sex-typicality and perceptions of attractiveness, evidence for a link between sex-typicality and perceptions of facial health is relatively convincing. Men with more masculine faces and women with more feminine faces are perceived as looking healthier (Boothroyd et al., 2013; Gray & Boothroyd, 2012; Zebrowitz & Rhodes, 2004) and these findings extend to non-Western samples (Scott et al., 2008). Additionally, Smith et al. (2009) found that participants showed stronger preferences for sex-typicality in faces displaying high apparent health than in faces displaying low apparent health. Smith et al.'s (2009) finding suggests there may be some "cross-talk" between sexual dimorphism and other health cues when people judge the health of faces. By contrast with the above results, Boothroyd et al. (2005) found that preferences for perceived health and masculinity in men's faces were unrelated in two samples of women, suggesting that preferences for these two cues may be at least partly independent (see also Jones et al., 2005).

While the studies described above investigated a possible relationship between facial sex-typicality and apparent health in faces (i.e., *perceived* facial health), other work has examined possible links between facial sex-typicality and putative measures of actual health. Evidence for a relationship between masculinity in men's faces and actual health is mixed, however. Rhodes et al. (2003a) found that rated facial masculinity correlated positively with general health in male adolescents based on a composite score derived from health professionals' evaluations of historical medical records. Consistent with this result, other research has found that men with more masculine faces reported experiencing a lower incidence of colds and flu (Boothroyd et al., 2013; Thornhill & Gangestad, 2006) and lower antibiotic use (Thornhill & Gangestad, 2006). It should be noted, however, that facial masculinity was unrelated to men's antibiotic use in Boothroyd et al.'s (2013) sample. Additionally, neither Boothroyd et al. (2013) nor Thornhill and Gangestad (2006) found evidence of a significant relationship between facial masculinity and the number of stomach infections reported by male participants. While these studies used self-reported medical history to assess the link between facial masculinity and measures of health, other work has investigated the link between facial masculinity and a more direct measure of men's immune function. Rantala et al. (2013a) found that masculinity in men's faces was associated with a stronger antibody response following a hepatitis B vaccination.

In women, evidence for a link between facial femininity and actual health is equally mixed. Studies have shown that facial femininity is negatively correlated with the number of respiratory infections reported by female participants (Gray & Boothroyd, 2012; Thornhill & Gangestad, 2006). Neither Gray and Boothroyd (2012) nor Thornhill & Gangestad (2006) observed a significant relationship between facial femininity and self-reported number of stomach infections, however. These two studies report conflicting findings for a link between facial femininity and women's antibiotic use, however, with Gray and Boothroyd (2012) reporting a significant negative relationship and Thornhill and Gangestad (2006) reporting no significant relationship. Adding to the null results within the literature, Rhodes et al. (2003a) found that rated facial femininity was unrelated to actual health in female adolescents.

Is facial adiposity related to attractiveness and health?

It is well established that obesity, typically indexed by body mass index (BMI, weight scaled for height), is linked to a number of health risks, such as type II diabetes and cardiovascular diseases (for a review see Guh et al., 2009). BMI has been shown to predict male and female bodily attractiveness; normal weight bodies (BMI 18.5 – 24.99 kg/m^2; World Health Organization, 2000) tend to be judged as optimally attractive (see e.g., Weeden & Sabini, 2005 for a review). Facial adiposity, or perception of weight in the face, is positively correlated with BMI (Coetzee et al., 2009; Han et al., 2016; Tinlin et al., 2013) and people can accurately estimate others' weight based on their face alone (Coetzee et al., 2009). Taken together, these findings have led many researchers to suggest that facial adiposity is a potential cue to attractiveness and health in humans.

Indeed, recent research suggests that facial cues of adiposity play an important role in attractiveness judgments. Relatively low levels of adiposity in male and female faces tend to be perceived as attractive in Western (Coetzee et al., 2009; Han et al., 2016; Rantala et al., 2013a, 2013b) and African (Coetzee et al., 2012) populations. However, some work suggests that preferences for facial adiposity may be malleable and influenced by factors such as environmental harshness. Batres and Perrett (2016) observed a significant within-person effect of environmental harshness on men's, but not women's, adiposity preference. Male participants assigned to a training camp condition reported a stronger preference for cues of higher BMI in female faces, in addition to reporting an increase in multiple stressors (e.g., tiredness and pain). Despite this preference for a higher level of adiposity in the training camp condition, men's adiposity preference remained within the normal BMI category (<25 kg/m^2; World Health Organization, 2000) suggesting that although adiposity preferences may be contingent on factors such as environmental harshness, men tend to prefer facial cues of adiposity reflecting a healthy BMI.

Although the above findings point towards a widespread preference for faces displaying a relatively low level of facial adiposity, a mix of linear and curvilinear relationships between facial cues of adiposity and attractiveness have been reported. While Han et al. (2016) and Coetzee et al. (2012) found that BMI was linearly related to attractiveness, Coetzee et al. (2009) reported a curvilinear relationship whereby participants falling into the underweight (<18.5 kg/m^2) and overweight (>25 kg/ m^2) BMI categories (World Health Organization, 2000) received lower attractiveness ratings than their normal weight counterparts. These different types of relationships emerged despite all three samples containing comparable BMI ranges. Both linear and curvilinear relationships between adiposity and attractiveness have also been reported by studies measuring body fat percentage. While Rantala et al. (2013a) found that body fat percentage was linearly related to attractiveness, Rantala et al. (2013b) found a curvilinear relationship between body fat percentage and facial attractiveness.

The preference for thinner looking faces documented by some of the previous studies (Coetzee et al., 2012; Han et al., 2016; Rantala et al., 2013a) is consistent with the low 'ideal' BMI, particularly for women, portrayed by Westernized media (Spitzer et al., 1999; Tovée et al., 1997). Research suggests that the media's portrayal of a thin female body ideal has a greater impact on attractiveness judgments of female faces than it does on health judgments (Coetzee & Perrett, 2011). Coetzee and Perrett (2011) found that women exhibited stronger preferences for thinner looking female faces when assessing attractiveness than when assessing health. By contrast, men did not differentiate between the level of facial adiposity they considered to be optimally attractive and healthy in female faces. Despite this significant interaction between judgment type and rater sex, Coetzee and Perrett (2011) found no sex difference in what men and women judged to be the 'most attractive' and 'most healthy' level of facial adiposity, with both sexes reporting a preference for facial appearance within the healthy BMI range (18.5 – 24.99 kg/m^2; World Health

Organization, 2000). A link between facial adiposity and judgments of health has been documented by several other perceptual studies. Research shows that thinner looking adult faces tend to be judged as healthier in British (Coetzee et al., 2009, 2011) and African (Coetzee et al., 2012) populations.

In line with the above evidence linking facial cues of adiposity to health perceptions and evidence linking BMI to measures of health (see Guh et al., 2009 for a review), a growing body of work has documented correlations between facial cues of adiposity and actual health. Perceived facial adiposity has been shown to communicate information about health over and above that which is explained by BMI (Tinlin et al., 2013) and facial adiposity correlates more strongly with certain aspects of health (such as reported frequency and duration of respiratory infections) than BMI does (Coetzee et al., 2009). Individuals with thinner looking faces experience fewer and shorter-lasting bouts of cold and flu, report lower use of antibiotics, and score higher on measures of cardiovascular health (Coetzee et al., 2009). Similarly, Tinlin et al. (2013) found that perceived facial adiposity predicted women's scores on a composite measure of general condition derived from items assessing their physical and psychological health. Furthermore, ratings of facial adiposity during adolescence have been shown to predict adulthood risk of obesity, chronic conditions such as arthritis and diabetes, and all-cause mortality (Reither et al., 2009). Han et al. (2016) also found no significant relationship between ratings of women's facial adiposity and their salivary cortisol levels.

Is facial coloration related to attractiveness and health?

Consistent with work suggesting that facial coloration plays an important role in social interactions in many non-human primate species (see e.g., Setchell et al., 2006; Waitt et al., 2003), recent research suggests that facial skin coloration also plays an important role in human social interaction. Studies investigating the effect of human facial coloration on social judgments have typically assessed skin color using spectrophotometer measurements in CIELab color space (Commission Internationale de l´Eclairage, 1976). Modelled on the human visual system, CIELab color space comprises three independent color axes: lightness (L*), red (a*), and yellow (b*). Increasing redness and yellowness in male and female face images increases ratings of attractiveness (Re et al., 2011a, Whitehead et al., 2012a, Whitehead et al., 2012b). Consistent with these findings for a link between skin redness and attractiveness, Stephen et al. (2012a) found that increasing skin redness (while holding lightness and yellowness constant) enhances perceived attractiveness, dominance, and aggression in men's faces. Very high levels of redness in men's faces increased the appearance of aggression to the detriment of attractiveness, however (Stephen et al., 2012a).

Other work investigating the link between facial skin coloration and attractiveness has examined the role of skin color *distribution* in attractiveness judgments. Skin color homogeneity is positively correlated with perceptions of youthfulness and attractiveness in male (Fink et al., 2012) and female (Fink et al., 2006b; Matts et al., 2007) faces. These studies identified melanin (one of two major pigments known to influence skin yellowness) as an important contributor to smoothness of skin color distribution. Recent research suggests the *amount* of melanin coloration in faces affects perceptions of attractiveness. In a forced-choice paradigm, Lefevre and Perrett (2014) found that faces with high melanin coloration were significantly preferred over faces with low melanin coloration.

Research suggesting that melanin coloration leads to more positive evaluations of faces extends to perceptions of health as well as attractiveness. Participants tend to increase melanin coloration when completing tasks instructing them to maximise the healthy appearance of Caucasian faces (Stephen et al., 2011; Whitehead et al., 2012c). Some studies suggest that the perceived health of faces may be more strongly influenced by carotenoid-associated coloration than melanin-associated coloration, however. While the processes of melanization (i.e., tanning) and carotenoid ingestion both lead to increases in skin yellowness, melanization also leads to a decrease in skin lightness (Stamatas et al., 2004). Stephen et al. (2011) found that participants opted to increase carotenoid coloration more than melanin coloration in Caucasian faces in order to enhance healthy appearance. Similarly, Lefevre and Perrett (2014) found stronger preferences for carotenoid coloration than for melanin coloration in Caucasian faces. This effect was also sex-specific; the carotenoid preference was stronger than the melanin preference in female faces relative to male faces, regardless of the sex of observer (Lefevre & Perrett, 2014). The link between carotenoid coloration and perceived health extends to African (Stephen et al., 2011) and Asian (Whitehead et al., 2012b) populations.

In keeping with evidence suggesting that facial skin coloration influences perceptions of health, Stephen et al. (2009a) found that increasing the redness, yellowness, and (to a lesser extent) lightness of faces in CIELab color space led to more positive evaluations of health. Additionally, some studies have demonstrated that homogenous skin color distribution is associated with health perceptions, whereby greater evenness of melanin and, in particular, haemoglobin distributions leads to an increase in health ratings (Fink et al., 2012; Matts et al., 2007). That haemoglobin distribution influences the perceived health of faces is consistent with other work showing that oxygenated-blood coloration (i.e., skin redness) in faces is perceived as healthy (Re et al., 2011a). A recent study by Henderson et al. (2016) found that skin yellowness, but not redness or lightness, positively correlated with perceived health, however. Similarly, Jones et al. (2016) found that global skin yellowness predicted the perceived health of faces. The coloration of specific facial regions has also been linked to health perceptions; periorbital (i.e., under eye) luminance and cheek redness both predict apparent health (Jones et al., 2016).

Since skin coloration is a malleable facial cue with the potential to change in a short period of time (e.g., in response to illness), it has been argued that aspects of facial skin coloration convey information about actual health. Indeed, redness and yellowness in Caucasian faces is associated with cardiovascular health (Stephen et al., 2009a) and good diet (Stephen et al., a; Whitehead et al., 2012a). Cross-culturally extending findings for a link between facial skin coloration and diet, Tan et al. (2015) found that skin yellowness and (to a lesser extent) redness increased in an Asian population following a six-week dietary intervention whereby participants increased their daily carotenoid intake. As antioxidants, carotenoids are crucial for skin health and insufficient dietary intake can trigger conditions associated with heightened oxidative stress (see e.g., Frisard & Ravussin, 2006; Sies et al., 2005). Further, carotenoids deficits can lead to immune suppression due to the importance of their role in immune-cell activity (Bendich, 1991). Nevertheless, there is no evidence to date of a direct link between carotenoid-coloration in faces and immune response. There is, however, evidence linking men's facial skin health to a measure of their underlying physical condition. Roberts et al. (2005) found that MHC heterozygosity predicted the apparent health of men's facial skin, suggesting that skin coloration (in addition to other surface information) serves as a cue to immunocompetence.

The current studies

The following four empirical chapters present studies investigating various aspects of the role of adiposity cues in face preferences and perceptions. Specifically, they investigate (i) variation in preferences for facial cues of adiposity and whether these preferences predict actual partner choice, (ii) the relationship between preferences for facial cues of adiposity and pathogen disgust, (iii) whether individuals integrate information from shape cues of adiposity with information from other health cues when judging the attractiveness and health of faces, and (iv) the interrelationships among women's sociosexual orientation, BMI, waist-hip ratio, and facial attractiveness.

Studies of population health have frequently reported evidence of assortative mating for adiposity, whereby levels of adiposity in romantic couples tend to be positively correlated (see Di Castelnuovo et al., 2009 for a meta-analytic review). Importantly, assortative mating for adiposity may have ramifications for population health resulting from the joint effect of partners' levels of adiposity on fertility and/or offspring health. Indeed, evidence suggests there is a substantial heritable component to adiposity (reviewed in Speliotes et al., 2010). Consequently, assortative mating for adiposity has the potential to increase the percentage of obese individuals in the population (Hebebrand et al., 2000; Speakman et al., 2007). In addition to the likelihood of increasing obesity rates, assortative mating for adiposity has been found to impact negatively on the fertility of couples, with overweight/obese couples more likely to experience difficulty conceiving (Ramlau-Hansen et al., 2007). In light of the above findings, many researchers have emphasized the importance of identifying contributing factors to assortative mating for adiposity (Courtiol et al., 2010; Di Castelnuovo et al., 2009; Hebebrand et al., 2000; Speakman et al., 2007).

One possible explanation for the positive correlation between romantic partners' levels of adiposity is that people pair with individuals displaying similar levels of adiposity due to assortative *preferences* for cues of adiposity (i.e., leaner people show stronger preferences for leaner individuals). Evidence for assortative preferences for cues of adiposity is somewhat mixed, however. Some studies have reported assortative preferences for bodily cues of adiposity, whereby people with leaner body shapes show stronger preferences for leaner bodies (Courtiol et al., 2010; Tovée et al., 2000). On the contrary, other studies have found that measures of own adiposity do not predict mating-related perceptions of body images (Han et al., 1999; Price et al., 2013). One commonality among these studies is their exclusive focus on cues of body attractiveness while obscuring facial characteristics including cues of adiposity, which are known to communicate information important for partner choice. Indeed, facial cues of adiposity convey information about an individual's physical attractiveness (Coetzee et al., 2009; Hume & Montgomerie, 2001), physical health (Coetzee et al., 2009; Tinlin et al., 2013), immunocompetence (Rantala et al., 2013a), life expectancy (Reither et al., 2009), and psychological condition (Tinlin et al., 2013). Taken alongside findings suggesting that more importance is assigned to the face than to body characteristics when assessing attractiveness (e.g., Confer et al., 2010; Currie & Little, 2009; Peters et al., 2007), these results raise the possibility that individual differences in preferences for *facial* cues of adiposity play a role in assortative mating for adiposity. Consequently, my first empirical chapter examines the contribution of individual differences in preferences for cues of adiposity in opposite-sex faces to assortative mating for adiposity.

Chapter 3 further explores individual differences in facial adiposity preferences by examining a potential underlying mechanism causing this systematic variation: pathogen disgust (i.e., disgust experienced in response to potential sources of pathogens). Individual differences in pathogen disgust, which are typically assessed using the pathogen disgust subscale of the Three Domains of Disgust Scale (TDDS, Tybur et al., 2009), have previously been linked to face preferences. Jones et al. (2013a, 2013b) found that individuals who reported particularly strong concerns about infectious disease tended to display stronger aversions to facial cues related to poor health (e.g., reduced sex-typical shape characteristics). Other work suggests that pathogen disgust is a reliable predictor of men's but not women's preferences for putative health cues (Lee et al., 2013). These correlational findings are complemented by research demonstrating that experimentally priming concerns about infectious disease increases preferences for putative health cues in potential mates (Little et al., 2011c).

Other research into the psychological mechanisms involved in pathogen avoidance has focused on the stigmatization of obese individuals. In post-industrialized societies, obese individuals have been shown to elicit pathogen disgust (Lieberman et al., 2011), and the strength of negative attitudes about obese individuals are positively correlated with concerns about infectious disease (Park et al., 2007). In light of these findings and studies showing that facial adiposity is negatively correlated with perceived health (Coetzee et al., 2009), actual physical health (Coetzee et al., 2009; Tinlin et al., 2013), and immunocompetence (Rantala et al., 2013a), it is possible that individuals who are particularly concerned about infectious disease will display greater aversions to faces displaying higher levels of facial adiposity. My second empirical chapter investigates this possibility by testing for a relationship between men and women's pathogen disgust and their attractiveness judgments of faces differing in cues of BMI.

While Chapters 2 and 3 examine whether individual differences in adiposity preferences exist and whether pathogen disgust is a potential source of such differences, Chapter 4 examines how individuals integrate information from facial cues of adiposity with other health-related information contained in the face. Research into the mate preferences of non-human animals suggests there are interactions between the effects of cues to different aspects of physical condition, potentially increasing the reliability with which individuals can evaluate the condition of others (Candolin, 2003). Little is known about interactions between the effects of health-related cues in humans, however.

Despite the association between low levels of facial adiposity and good long-term health (Coetzee et al., 2009; Reither et al., 2009; Tinlin et al., 2013), low levels of adiposity are also symptomatic of various infectious diseases, such as malaria (Girard et al., 2007) and gastroenteritis (Glass et al., 2009; Kahan et al., 2011). Consequently, it is important that people are able to detect whether individuals displaying low levels of adiposity do so because they are in good physical condition or because they are ill. One possible route to making this distinction could be integrating information from facial cues of adiposity with information from other putative health cues, such as facial coloration. Indeed, recent research points towards facial skin coloration as a valid cue to physical condition, with studies reporting that skin yellowness and redness are linked to good diet and cardiovascular health, respectively (Stephen et al., 2009b, 2011; Whitehead et al., 2012). Chapter 4 investigates the possibility that people use facial color cues to disambiguate whether individuals displaying low levels of adiposity do so because they are healthy or because they are ill.

Although most research examining the link between facial adiposity and attractiveness has focused on the function of adiposity as a health cue, it is possible that adiposity cues also communicate information about mating-related behaviours. Given that (i) adiposity cues play an important role in assessments of physical attractiveness (Coetzee et al., 2009, 2012; Han et al., 2016; Rantala et al., 2013a, 2013b), and (ii) some research has found that women's physical attractiveness predicts their openness to short-term sexual relationships (i.e., their sociosexual orientation; Boothroyd et al., 2008, 2011), Chapter 5 investigates whether adiposity contains information about women's sociosexual orientation.

Although some studies have reported positive correlations between women's physical attractiveness and their scores on the Sociosexual Orientation Inventory (Boothroyd et al., 2008, 2011), other studies have reported null findings for such a link (Clark, 2004; Penke & Asendorpf, 2008; Perilloux et al., 2013). These mixed findings could potentially be a consequence of studies not controlling for the effects of cosmetics on attractiveness ratings (see, e.g., Etcoff et al., 2011), in turn creating or obscuring correlations between sociosexual orientation and facial attractiveness. Findings for a significant positive relationship between facial attractiveness and SOI are reported by studies using composite faces as opposed to real face images (Boothroyd et al., 2008, 2011) and, consequently, these results may not necessarily generalize to ratings of individual faces. Of all the studies testing for a link between women's facial attractiveness and sociosexual orientation, only two assessed sociosexual orientation using the most recent version of the Sociosexual Orientation

Inventory, the SOI-R (Penke & Asendorpf, 2008; Perilloux et al., 2013), and neither of these studies found evidence for a significant relationship between women's attractiveness and sociosexual orientation.

In light of the above, Chapter 5 addresses some of the methodological issues of previous studies by investigating the relationship between multiple measures of women's physical attractiveness and their scores on Penke and Asendorpf's (2008) revised version of the Sociosexual Orientation Inventory (SOI-R) using the largest sample of women tested to date. In addition to testing for a link between women's facial attractiveness and their scores on the SOI-R, Chapter 5 also tests for possible relationships between their SOI-R scores and two body measures known play an important role in judgments of women's attractiveness: body mass index and waist-hip ratio (reviewed in Weeden & Sabini, 2005).

Ethics and General Methodology

All procedures in Chapters 2–5 were approved by the Science and Engineering Ethics Committee at the University of Glasgow. Participants provided experiment and photographic consent before beginning the study. The photographic consent form asked participants to specify whether or not we could use their face photographs in a laboratory setting and/or online. This form stated that, depending on how participants consented to have their images used, their faces might be rated by others for various social traits (e.g., health and attractiveness) in future studies. Participants were also offered the opportunity to change or withdraw their photographic consent at any point of the study.

The work in this thesis is based on three sets of faces. Face set 1 (Chapters 2 and 3) is a set of face images purchased by the Face Lab from the 3dsk online database where the individuals provided full photographic consent. Set 2 (Chapter 4) is a subset of facial images collected from the Perception Lab at the University of St Andrews, with participants consenting to have their images used in composite face images. Set 3 (Chapter 5) was collected at the University of Glasgow as part of the current thesis, with participants consenting to have their images used online.

Given that emotional expressions are known to influence social perceptions (see Main et al. 2010, for a review), neutral face images were used in all four empirical chapters to control for effects of facial expression. Third-party ratings of faces were used in this thesis because ratings of face images are a reliable way of assessing people’s mate preferences (for evidence of a link between face preferences and partner choice, see DeBruine et al., 2012) and strong inter-rater reliability has been reported in studies using attractiveness ratings of face images, even among raters from different cultures (e.g., Langlois et al., 2000). Given that facial measurements of 2D images (e.g., facial width-to-height ratio) may be error prone due to difficulties controlling for factors such as head tilt (Schneider et al., 2012), facial measurements were not assessed in this thesis.

Participants in all four empirical chapters reported being heterosexual. This thesis focuses exclusively on heterosexual people's mate preferences because prior work on the link between attractiveness and adiposity generated hypotheses based on sexual selection theory. Indeed, the rationale to study assortative mating for BMI in Chapter 2 is partly due to the genetic component associated with obesity and assortative mating for BMI and this is primarily relevant to heterosexual couples. Although there is great need for more studies looking at the face preferences and mating strategies of homosexual, bisexual, and pansexual people, this is beyond the scope of the current work.

An advantage of using real face images in Chapters 2, 3, and 5 is that the results are potentially more informative about real world interactions than results from studies using composite or manipulated face images. Chapter 2 investigates whether face preferences reported in a laboratory setting translate to real world mating decisions by examining the relationship between face preferences and actual partner choice. The cross-sectional design of the study presented in Chapter 2 limits conclusions about a possible causal relationship between preference and choice, however. Although conducting a longitudinal study tracking people's mate preferences and partner choice would have been more informative about the causal direction of a relationship between these two variables, conducting a longitudinal study of this nature was not feasible during my PhD studies.

One ethical consideration surrounding the use of real face images is whether measures should be implemented to reduce the chances of faces being rated by people who know the individual depicted in the face photograph. We addressed this potential issue by using face stimuli from a Slovakian image set in Chapters 2 and 3, thus limiting the likelihood that our UK participants were familiar with any of the faces. The face stimuli used in Chapter 5 were presented online at www.faceresearch.org, again reducing the likelihood that our online raters were familiar with the faces. We avoided collecting laboratory ratings of the face stimuli presented in Chapter 5 to minimize the possibility of male raters judging the short- or long-term attractiveness of women potentially from their University of Glasgow cohort.

In addition to using real face images in Chapters 2, 3, and 5, manipulated composite face images were used in Chapter 4. Composite faces were produced by averaging the shape, color, and texture information from color-calibrated (Hong et al., 2001) face images of three different individuals. This process yielded 10 unique composite male faces and 10 unique composite female faces (following Re & Perrett, 2014). The rationale for using this composite method in Chapter 4 was that we could then manipulate facial cues of BMI in faces that have a unique identity (i.e., are not recognisable as any of the identities that went into the composite face). Indeed, it may be unethical to manipulate adiposity in real faces and then obtain attractiveness ratings for heavier/lighter versions of faces recognisable as real individuals. Our use of composite face images addresses this potential ethical concern. Another strength of our methodological approach in Chapter 4 is that facial shape information was held constant during a color manipulation, and vice versa. Similarly, two out of three color dimensions within CIELab color space (CIE,

1976) were held constant during a color manipulation, with the third color dimension being increased or decreased. One caveat of this color manipulation, however, is that it does not account for skin homogeneity. Additionally, the composite face approach used in Chapter 4 limits the conclusions that can be drawn regarding how people combine information from facial color and shape cues in real faces.

In light of previous research demonstrating that face-only ratings are better independent predictors of overall attractiveness than body-only ratings (Bleske-Rechek et al., 2014), body ratings were not considered in this thesis. However, principle component analysis was used in Chapter 5 to investigate multiple measures of women's physical attractiveness (including facial attractiveness in short- and long-term contexts, BMI, and waist-hip ratio). Chapter 5 also addresses some of the methodological issues of earlier work by (i) using real face images as opposed to composite face images to strengthen ecological validity, (ii) controlling for the possible effects of makeup on attractiveness, (iii) using the SOI-R instead of an earlier version of this questionnaire that yielded inconsistent results, and (iv) having the largest sample size to date.

Chapter 2: Do assortative preferences contribute to assortative mating for adiposity?

This chapter is based on the following published paper:

Fisher, C. I., Fincher, C. L., Hahn, A. C., Little, A. C., DeBruine, L. M., & Jones, B. C. (2014). Do assortative preferences contribute to assortative mating for adiposity? *British Journal of Psychology*, *105*, 474-485.

Abstract

Assortative mating for adiposity, whereby levels of adiposity in romantic partners tend to be positively correlated, has implications for population health due to the combined effects of partners' levels of adiposity on fertility and/or offspring health. Although assortative *preferences* for cues of adiposity, whereby leaner people are inherently more attracted to leaner individuals, have been proposed as a factor in assortative mating for adiposity, there have been no direct tests of this issue. Because of this, and because of recent work suggesting that facial cues of adiposity convey information about others' health that may be particularly important for mate preferences, we tested the contribution of assortative preferences for facial cues of adiposity to assortative mating for adiposity (assessed from body mass index, BMI) in a sample of romantic couples. Romantic partners' BMIs were positively correlated and this correlation was not due to the effects of age or relationship duration. However, although men and women with leaner partners showed stronger preferences for cues of low levels of adiposity, controlling for these preferences did not weaken the correlation between partners' BMIs. Indeed, own BMI and preferences were

uncorrelated. These results suggest that assortative preferences for facial cues of adiposity contribute little (if at all) to assortative mating for adiposity.

Introduction

Assortative mating for adiposity, whereby levels of adiposity in romantic partners tend to be positively correlated, has frequently been reported in studies of population health (see Di Castelnuovo et al., 2009 for a meta-analytic review). Moreover, this correlation between levels of adiposity in romantic partners appears to be robust (Di Castelnuovo et al., 2009). For example, although correlations between levels of adiposity in romantic partners have typically been shown using body mass index (i.e., BMI, e.g., Jacobson et al., 2007; Silventoinen et al., 2003), they have also been demonstrated using other measures of adiposity, including dual-energy X-ray absorptiometry (Speakman et al., 2007) and skinfold thicknesses (Ginsburg et al., 1999). Moreover, assortative mating for adiposity does not appear to be an artifact of potential confounds. For example, although age and adiposity tend to be positively correlated (e.g., Pasco et al., 2012), as are romantic partners' ages (e.g., Watson et al., 2004), assortative mating for adiposity is not simply a by-product of the combined effects of these correlations (e.g., Speakman et al., 2007). Similarly, although socio-economic status and adiposity tend to be negatively correlated (e.g., Moore et al., 1997) and romantic couples tend to be from similar social backgrounds (e.g., Schwartz & Mare, 2005; Smits, 2003), combined effects of these correlations do not fully explain assortative mating for adiposity (e.g., Silventoinen et al., 2003). That the within-couples correlation between levels of adiposity appears to change very little as the duration of the relationship increases also suggests that assortative mating for adiposity is not simply due to the effects of the shared environment on adiposity (see Di Castelnuovo et al., 2009 for a meta-analytic review).

Importantly, assortative mating for adiposity could have serious consequences for population health. For example, since there is a substantial genetic component to adiposity (reviewed in Speliotes et al., 2010), assortative mating for adiposity may increase the proportion of individuals with high levels of adiposity (i.e., obese individuals) in the population (Hebebrand et al., 2000; Speakman et al., 2007). Indeed, some models of the effect of assortative mating for adiposity on the prevalence of obesity in a baseline population suggest that switching from random to completely assortative mating could more than double the percentage of obese individuals in the population within just two generations (Speakman et al., 2007). The combined effects of men's and women's adiposity on the fertility of couples (i.e., the tendency for infertility to be particularly common in couples where *both* the man and woman have high levels of adiposity) may counteract, to some extent, this effect of assortative mating on rates of obesity (Ramlau-Hansen et al., 2007). However, the combined effects of men's and women's adiposity on fertility also present additional evidence that assortative mating for adiposity can have negative effects on important aspects of population health (in this case, rates of infertility). In light of findings such as these, many researchers have emphasized the importance of establishing why assortative mating for adiposity occurs (Courtiol et al., 2010; Di Castelnuovo et al., 2009; Hebebrand et al., 2000; Speakman et al., 2007).

Assortative *preferences* for cues of adiposity, whereby leaner people show stronger preferences for leaner individuals, are a potential explanation for the positive correlation between romantic partners' levels of adiposity (e.g., Courtiol et al., 2010; Speakman et al., 2007; Zietsch et al., 2011). Indeed, assortative preferences for other physical characteristics have been reported in several studies of human mate preferences (reviewed in, e.g., Havlicek & Roberts, 2009) and assortative preferences are thought to play a critical role in assortative mating for physical characteristics in several non-human species (e.g., Møller, 1994). Furthermore, men's and women's preferences for leaner body shapes in silhouettes of opposite-sex bodies are negatively correlated with their actual romantic partner's BMI (Courtiol et al., 2010), although the cross-sectional design used in this work means that the causal direction of the relationship is unclear. Market-value-contingent preferences, whereby more attractive individuals demonstrate stronger preferences for attractive characteristics in images of potential mates (e.g., Little & Mannion, 2006), also suggest that assortative *preferences* for cues of adiposity could occur. However, while some work has suggested that preferences for cues of adiposity in body images are correlated with the perceiver's own BMI (Tovée et al., 2000), this effect of own BMI on attractiveness judgments appears to be largely due to atypical perceptions in individuals with eating disorders (e.g., anorexia nervosa, Tovée et al., 2000). Indeed, some other studies also suggest that measures of own adiposity, including BMI, do not predict mating-related perceptions of body images, such as perceptions of potential mates' health or youth (Han et al., 1999) and attractiveness (Price et al., 2013). Although these results are not necessarily conclusive, findings such as these suggest that own adiposity may have little effect on body adiposity preferences, at least in healthy individuals (Speakman et al., 2007), raising the possibility that assortative mating for adiposity is at least partly due to the additional constraints on the mate choices of individuals with higher levels of adiposity (see, e.g., Zietsch et al., 2011).

Despite the fact that there have been no direct empirical tests of the role of assortative preferences in assortative mating for adiposity, the lack of evidence for a robust relationship between own adiposity and mating-related perceptions of bodies has led some researchers to conclude that assortative preferences contribute little to assortative mating for adiposity (e.g., Speakman et al., 2007). However, focusing exclusively on *body* attractiveness may limit the conclusions that can be drawn about the role of mate preferences in assortative mating for adiposity. For example, although facial characteristics (including cues of adiposity) were obscured in the stimuli used in the above studies, *facial* cues of adiposity communicate information that is known to be important for human mate choice. For example, facial cues of adiposity communicate information about peoples' physical attractiveness (Coetzee et al., 2009; Hume & Montgomerie, 2001), perceived health (Coetzee et al., 2009), actual physical health (Coetzee et al., 2009; Tinlin et al., 2013), life expectancy (Reither et al., 2009), immunocompetence (Rantala et al., 2013), psychological condition (Tinlin et al., 2013), and hormonal profile (Tinlin et al., 2013). Indeed, perceived facial adiposity (i.e., the perception of fatness in the face) conveys information about health over and above that which is explained by BMI (Tinlin et al., 2013) and some aspects of health (e.g., reported frequency and duration of respiratory infections) are more strongly correlated with facial adiposity than they are with

BMI (Coetzee et al., 2009). Additionally, some studies suggest that facial cues are more important than body characteristics for judgments of men's and women's attractiveness, especially, but not exclusively, when bodies are clothed and when participants judged the attractiveness of potential mates for long-term relationships (e.g., Confer et al., 2010; Currie & Little, 2009; Peters et al., 2007). Together, these results raise the intriguing possibility that individual differences in preferences for *facial* cues of adiposity may play an important role in assortative mating for adiposity. However, no study to date has addressed the relationships between preferences for facial cues of adiposity and either own or actual partner characteristics. Perhaps more importantly, it is also not known whether individual differences in preferences for facial cues of adiposity contribute to assortative mating for adiposity.

In light of the above, we investigated the contribution of individual differences in preferences for cues of adiposity in opposite-sex faces to assortative mating for adiposity (measured using BMI). If controlling for the possible effects of individual differences in preferences for facial cues of adiposity weakens the positive correlation between romantic partners' BMIs, it would suggest that assortative preferences contribute to assortative mating for adiposity. However, if controlling for the possible effects of individual differences in preferences for cues of adiposity does not weaken the predicted correlation between romantic partners' BMIs, it would suggest that assortative preferences for facial cues of adiposity contribute little to assortative mating for adiposity. We assessed individual differences in preferences for facial cues of adiposity in two ways. One method measured participants' preferences for perceived facial adiposity.

The other measured participants' preferences for facial characteristics associated with actual BMI. Given the correlations between perceived facial adiposity and measured BMI that were reported in previous studies (Coetzee et al., 2009; Tinlin et al., 2013), these two measures of adiposity preference were expected to be highly correlated.

Methods

Participants

Sixty-two heterosexual couples were recruited for the study. The mean age of the men was 21.8 years (SD=1.96 years) and the mean age of the women was 21.2 years (SD=1.94 years). The average duration of these couples' relationships was 18.4 months (SD=15.1 months). Following Courtiol et al. (2010), the man and woman in each couple were tested at the same time, but were separated during testing.

Stimuli

The stimuli that we used to assess preferences for cues of adiposity in opposite-sex faces were full-color images of 50 white men (mean age=24.2 years, SD=3.99 years) and 50 white women (mean age=24.3 years, SD=4.01 years). All images were taken under standardized lighting conditions and against a constant background. All individuals photographed posed with neutral expressions and direct gaze. Images were standardized on pupil position and masked so that clothing was not visible. Height and weight measurements were taken from each of these 50 men (mean height=180.2 cm, SD=6.62 cm; mean weight=77.3 kg, SD=12.4 kg) and 50 women (mean height=168.6 cm, SD=6.48 cm; mean weight=57.2 kg, SD=11.4 kg).

The height and weight measurements were used to calculate each of the photographed individuals' BMI (men: M=23.7 kg/m^2, SD=3.13 kg/m^2, range=17.7-31.0 kg/m^2; women: M=20.1 kg/m^2, SD=3.66 kg/m^2, range=16.2-38.4 kg/m^2). According to the World Health Organization's (WHO) classifications (WHO, 2000), 28% of the women and 2% of the men were in the underweight BMI category (<18.5 kg/m^2), 68% of the women and 68% of the men were in the normal category (18.5–24.99 kg/m^2), and 4% of the women and 30% of the men were in the overweight category (>25 kg/m^2). None of these individuals were extremely underweight (i.e., none had BMI<15 kg/m^2, Bray, 1978) and only two individuals (both women) had BMI<17kg/m^2.

Methods for collecting ratings of facial adiposity were identical to those used in previous studies (Coetzee et al., 2009; Tinlin et al., 2013). The 50 male face images were rated for adiposity using a 1 (very underweight) to 7 (very overweight) scale by 60 heterosexual raters (30 women, 30 men; mean age=22.08 years, SD=3.53 years). The order in which images were presented was fully randomized. A different group of 60 heterosexual raters (30 women, 30 men; mean age=23.18 years, SD=3.04 years) rated the 50 female images for adiposity using the same scale. Inter-rater agreement was extremely high for adiposity ratings of both men's (Cronbach's alpha=.98) and women's (Cronbach's alpha=.98) faces. Consequently, we calculated the average adiposity rating for each face image (male faces: M=3.73, SD=0.76; female faces: M=3.79, SD=0.80). Men's and women's average ratings were highly correlated for both men's faces (r=.97, N=50, p<.001) and women's faces (r=.96, N=50, p<.001). Consistent with prior work (Coetzee et al., 2009; Tinlin et al., 2013), BMI and rated facial adiposity were positively correlated (men: r=.55, N=50, p<.001; women: r=.69, N=50, p<.001).

Procedure

Height and weight measurements were taken from each of the 62 men (mean height=180.6 cm, SD=6.55 cm; mean weight=77.1 kg, SD=11.2 kg) and 62 women (mean height=166.3 cm, SD=5.35 cm; mean weight=64.0 kg, SD=12.6 kg) who made up our romantic couples. These measurements were used to calculate BMI (men: M=23.6 kg/m^2, SD=3.13 kg/m^2, range=16.4–31.7 kg/m^2; women: M=23.1 kg/m^2, SD=4.19 kg/m^2, range=18.0–37.1 kg/m^2). According to the WHO (2000) classifications, 5% of the women and 5% of the men were in the underweight BMI category (<18.5 kg/m^2), 72% of the women and 69% of the men were in the normal category (18.5–24.99 kg/m^2), and 23% of the women and 26% of the men were in the overweight category (>25 kg/m^2). None of these individuals were extremely underweight (i.e., none had BMI<15 kg/m^2, Bray, 1978) and only one individual (a man) had BMI<17kg/m^2.

Each of the 62 men in our study rated the attractiveness of the 50 female faces described in our *Stimuli* section. Additionally, each of the 62 women in our study rated the attractiveness of the 50 male faces described in our *Stimuli* section. Attractiveness ratings were made using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. Following previous studies of preferences for facial cues of adiposity (e.g., Coetzee et al., 2009), the order in which images were presented was fully randomized and each image remained on screen until the participant had entered their rating. Inter-rater agreement, as measured by Cronbach's alpha, was high for both sets of ratings (both>.96).

Results

Calculating preference scores

For each couple, we calculated the Pearson product-moment correlation between (1) the woman's attractiveness rating for each of the 50 men's faces and those 50 men's rated facial adiposity (mean $r=-.16$, $SD=.17$, $p=.27$), (2) the woman's attractiveness rating for each of the 50 men's faces and those 50 men's BMI (mean $r=-.13$, $SD=.13$, $p=.37$), (3) the man's attractiveness rating for each of the 50 women's faces and those 50 women's rated facial adiposity (mean $r=-.23$, $SD=.14$, $p=.11$), and (4) the man's attractiveness rating for each of the 50 women's faces and those 50 women's BMI (mean $r=-.27$, $SD=.10$, $p=.058$)[1]. Note that this procedure produces two correlation coefficients for each participant (one being a measure of their preference for perceived facial adiposity and the other a measure of their preference for facial cues of BMI). These correlation coefficient scores served as the dependent variables in subsequent analyses. For each of these preference scores, larger positive values indicate stronger preferences for facial characteristics associated with

[1] One exemplar in the sample of women's faces had particularly high BMI (38.4 kg/m^2) and was identified as a potential outlier who could unduly influence preference scores. However, men's BMI preference scores when this exemplar was included and excluded were highly correlated ($r=.80$, $N=62$, $p<.001$). More importantly, the patterns of results in subsequent analyses were identical when men's BMI preference scores were calculated with this exemplar excluded. Consequently, we have not excluded this exemplar from the main analyses reported here.

higher BMI and larger negative values indicate stronger preferences for facial characteristics associated with lower BMI.

Next, we analyzed women's preference scores (i.e., their preferences for perceived facial adiposity and their preferences for facial cues of BMI) using factor analysis. This analysis produced a single factor that explained 87% of the variance in women's preference scores and was highly correlated with both of the original variables (both r=.93). We labeled this factor *women's preference for cues of BMI in men's faces.* A corresponding analysis for men's preference scores also produced a single factor. This factor explained 89% of the variance in men's preference scores and was highly correlated with both of the original variables (both r=.94). We labeled this factor *men's preference for cues of BMI in women's faces.* On both of these factors, higher scores indicate stronger preferences for facial characteristics associated with higher BMI. Romantic partners' preferences for cues of BMI in opposite-sex faces were positively correlated (r=.31, N=62, p=.016).

Assortative mating for BMI in our sample

We first tested for evidence of assortative mating for BMI in our sample. As predicted, romantic partners' BMIs were positively correlated (r=.49, N=62, p<.001). Subsequent partial correlation analyses showed that this correlation between romantic partners' BMIs remained significant when we controlled for the possible effects of women's age (partial r=.38, p=.003), men's age (partial r=.45, p<.001), or both men's age and women's age simultaneously (partial r=.38, p=.003). These results show that assortative mating for BMI in this sample is not due to the combined effects of older individuals tending to have higher BMI and couples tending to be similar in age. Similarly, results for a partial analysis controlling for the possible effects of relationship duration (partial $r=.45$, $p<.001$) suggested that relationship duration had little effect on the strength of assortative mating for BMI in this sample.

Assortative preferences and assortative mating for BMI

To investigate whether individual differences in preferences for cues of BMI in opposite-sex faces contributed to assortative mating for BMI, we conducted a second set of partial correlation analyses. These analyses showed that the correlation between romantic partners' BMIs ($r=.49$, $N=62$, $p<.001$) changed very little when we controlled for the possible effects of women's preferences for cues of BMI in men's faces (partial $r=.50$, $p<.001$), men's preferences for cues of BMI in women's faces (partial $r=.47$, $p<.001$), both men's and women's preferences for cues of BMI in opposite-sex faces simultaneously (partial $r=.50$, $p<.001$), or the average of men's and women's preferences for cues of BMI in opposite-sex faces (partial $r=.47$, $p<.001$). These results suggest that individual differences in preferences for facial cues of BMI contributed little (if at all) to assortative mating for BMI.

Preferences for cues of BMI and own / partner's BMI

Although our results suggest that individual differences in preferences for facial cues of BMI contribute little to assortative mating for BMI, it is still possible that participants' preferences for cues of BMI in opposite-sex faces are correlated with either their own BMI or their partner's BMI. Thus, we investigated the intercorrelations among men's BMI, women's BMI, men's preferences for cues of BMI in women's faces, and women's preferences for cues of BMI in men's faces (Table 1). Men's and women's preferences for cues of BMI in opposite-sex faces predicted their romantic partner's BMI (men's preferences: $r=.30$, $N=62$, $p=.017$; women's preferences: $r=.30$, $N=62$, $p=.017$), indicating the individuals who showed stronger preferences for cues of low BMI in opposite-sex faces had leaner romantic partners. By contrast with these results for partner's BMI, own BMI predicted neither men's nor women's preferences for facial cues of BMI (men's preferences: $r=.17$, $N=62$, $p=.19$; women's preferences: $r=.04$, $N=62$, $p=.77$).

Table 1. Correlations among men's BMI, women's BMI, men's preferences for cues of BMI in women's faces, and women's preferences for cues of BMI in men's faces.

	Women's BMI	**Men's preference for cues of BMI**	**Women's preference for cues of BMI**
Men's BMI	.49***	.17 ^{NS}	.30*
Women's BMI		.30*	.04^{NS}
Men's preference for cues of BMI			.31*

N=62 for each correlation, *** p<.001, ** p<.01, * p<.05, ^{NS} p>.05 (all non-significant correlations were p>.19)

Finally, we conducted regression analyses to test whether preferences for cues of BMI in opposite-sex faces and own BMI *independently* predicted actual romantic partner's BMI. Partner's BMI was entered as the dependent variable and own BMI and preferences for cues of BMI were entered simultaneously as predictors. Separate regression analyses were conducted for men and women. For men, their own BMI (t=4.04, standardized beta=.45, p<.001) and their preference for cues of BMI in women's faces (t=2.03, standardized beta=.23, p=.047) each independently predicted their romantic partner's BMI. This pattern was also observed for women; own BMI (t=4.43, standardized beta=.48, p<.001) and preference for cues of BMI in men's faces (t=2.63, standardized beta=.28, p=.011) each independently predicted their romantic partner's BMI. Stepwise versions of these analyses showed that adding preferences to a model in which only own BMI was a predictor significantly increased the variance in partner BMI explained by the model (men's preferences: R^2 change = .05, p = .047; women's preferences: R^2 change = .08, p = .011).

Discussion

As in many previous studies that have reported assortative mating for adiposity (see Di Castelnuovo et al., 2009 for a meta-analytic review), romantic partners' BMIs were positively correlated. Partial correlation analyses showed that this correlation between romantic partners' BMIs was not due to the possible effects of age or relationship duration (see also, e.g., Di Castelnuovo et al., 2009 and Speakman et al., 2007).

Consistent with previous work showing that men's and women's preferences for leaner *body* images were correlated with their actual romantic partner's BMI (Courtiol et al., 2010), men's and women's preferences for facial cues of BMI in opposite-sex faces were correlated with their romantic partners' BMIs; people with leaner partners showed stronger preferences for cues of low BMI in opposite-sex faces. Additionally, romantic partners' preferences for cues of BMI in opposite-sex faces were concordant; the romantic partners of people who had particularly strong preferences for cues of low BMI also tended to demonstrate stronger preferences for these facial cues. Despite these significant correlations between BMI preferences and partner's BMI and between romantic partners' BMI preferences, we found no evidence that individual differences in preferences for facial cues of BMI contributed to assortative mating for BMI. Indeed, controlling for the possible effects of assortative preferences for cues of BMI had no discernible effect on the correlation between romantic partners' BMIs. Additional analyses indicated that this pattern of results was due to the independence of own BMI and preferences for facial cues of BMI; own BMI and preference for facial cues of BMI were not significantly correlated in our sample and independently predicted partner's BMI in both men and women. In other words, while preferences for cues of BMI in opposite-sex faces explained some of the variance in the adiposity of men's and women's romantic partners, this variance was wholly independent of that which was explained by assortative mating for BMI. Together, these results then suggest that *assortative preferences* contribute little (if at all) to *assortative mating* for adiposity. That own BMI and preference for facial cues of BMI were not significantly correlated in our sample is consistent with other recent work that observed no significant correlations between measures of participants' own adiposity and their preferences for cues of adiposity in opposite-sex bodies (Price et al., 2013).

Although factors not considered in our study will almost certainly contribute to assortative mating for adiposity (e.g., social homogamy, Silventoinen et al., 2003), our results are consistent with the proposal that assortative mating for adiposity is not due to assortative preferences for cues of adiposity, but is likely to be due (at least in part) to the additional constraints on the mate choices of individuals with higher levels of adiposity (Speakman et al., 2007; see also Zietsch et al., 2011). Additional constraints on the mate choices of individuals with higher levels of adiposity may arise because the pool of people who are willing to choose mates with higher levels of adiposity will be smaller (and include a higher proportion of fatter individuals) than the pool of people who are willing to choose relatively lean mates (Speakman et al., 2007). Indeed, individuals with higher levels of adiposity do report having had fewer sexual partners in the previous year, consistent with the proposal that their mate choices are more constrained (e.g., Bajos et al., 2010). Our results are also consistent with recent research on the genetic basis of assortative mating for BMI, which suggests that it is more likely to be due to the heritability of BMI than heritability of preferences for cues of BMI (Zietsch et al., 2011).

Findings for attractiveness judgments of opposite-sex faces are often assumed to give insight into the factors that influence human mate choice (for reviews see Gangestad & Thornhill, 2008; Little et al., 2011b; Rhodes, 2006) and are frequently interpreted as evidence that sexual selection has been an important factor in the evolution of human face preferences (Gangestad & Thornhill, 2008; Little et al., 2011b; Rhodes, 2006). However, many researchers have noted that few studies have investigated the possible correlations between face preferences and actual partner choice (e.g., Penton-Voak, 2011; Puts et al., 2012). Our data show that preferences are linked to real-life mate choice since they demonstrate correlations between partner BMI and both men's and women's face preferences, revealing a pathway through which sexual selection could have influenced preferences for facial cues of adiposity. Although the conclusions that can be drawn on this point from our data are limited to conclusions relating to preferences for facial cues of adiposity, similar tests involving preferences for other facial characteristics (e.g., sex-stereotypical shape cues) may provide converging evidence for links between face preferences and romantic partner choice (see, e.g., DeBruine et al., 2012).

There are several limitations to our study that should be acknowledged. First, the cross-sectional design of our study means that the causal direction of the relationship between face preferences and partner BMI is unclear. Studies using longitudinal designs to investigate this issue may clarify whether mate preferences directly influence mate choices, mate choices directly influence mate preferences, or both. Second, the ranges of BMIs represented in our stimuli and our participant couples were relatively narrow (e.g., did not include many obese individuals). Further studies with a greater proportion of overweight and obese individuals could yet implicate assortative preferences in assortative mating for adiposity. Such studies could also use face stimuli that were more closely matched in age to the participants than was the case in the current study where the faces were, on average, between two and three years older than the participants. Third, we used a subjective measure of facial adiposity that, although positively correlated with actual BMI, may still be subject to perceptual biases (e.g., attractiveness halo effects, Dion et al., 1972). Subsequent studies exploring individual differences in preferences for facial cues of BMI may consider employing more objective measures of facial adiposity. However, although some facial metric measures of adiposity have been developed that correlate reasonably well with actual BMI (see Coetzee et al., 2010), these measures can be subject to systematic errors (see Schneider et al., 2012). Further work is needed to develop more robust, objective measures of facial adiposity. Fourth, although our analyses reveal individual differences in preferences for facial correlates of BMI, it is unclear whether these individual differences reflect variation in motivation to obtain mates with low BMI or variation in motivation to obtain mates who, for example, lead particular lifestyles or possess particular hormonal profiles that are correlated with BMI. Studies investigating the determinants of individual differences in preferences for cues of BMI may clarify this issue.

This study directly tested the contribution of assortative preferences for cues of BMI in opposite-sex faces to assortative mating for adiposity in a sample of romantic couples. Analyses suggested that individual differences in preferences for facial cues of BMI contribute little (if at all) to assortative mating for BMI. However, both men’s and women’s preferences for facial cues of BMI were positively correlated with their actual romantic partners’ BMIs. Thus, our data potentially implicate preferences for cues of BMI in partner choices but also show that partner choice is not redundant with face preferences, at least with regard to preferences for cues of BMI. Indeed, some differences between preferences for cues of BMI and actual mate choices would be expected, given that mate choices are likely to be constrained in ways that mate preferences are not. Importantly, the causal direction of the relationship between preferences for facial cues of BMI and partner BMI is unclear. One possibility is that preferences for cues of adiposity directly contribute to partner selection (i.e., preferring cues associated with lower BMI causes people to choose leaner partners). Another possibility is that having a leaner partner causes people to prefer cues of lower levels of facial adiposity. For example, people may realign their preferences to match partner characteristics in order to reduce cognitive dissonance and experiments have demonstrated that increasing participants' recent visual experience with images of the bodies of individuals with higher levels of adiposity increases their preferences for facial characteristics that are correlated with higher BMIs (Re et al., 2011b). That these possibilities are by no means mutually exclusive may have important implications for the mechanisms and processes through which individuals' mate preferences develop. For example, people typically have more than one romantic partner in the course of their lives (e.g., Brown & Sinclair, 1999). Consequently, if current partner choice influences preferences, these preferences may influence future partner choice, establishing a feedback loop that amplifies the effects of early mate choices on partner choice later in life. Consistent with this proposal, recent work has found that characteristics of participants' sexual experiences that occurred early in adulthood predicted their physical and emotional satisfaction with their current sexual interactions, even when the effects of global sexual satisfaction were controlled for statistically (Smith & Schaffer, 2013). While work on the development of human mate preferences has typically focused on experiences in early life (e.g., imprinting-like effects in childhood, Perrett et al., 2002), the possibility that early mate choices are another important factor for the development of mate preferences has received relatively little attention. We suggest that studies directly testing the role of previous mate choices in future mate choice and mate preferences may provide important insights into the ontogeny of mating behavior.

The current chapter found that partner's BMI was correlated with preference for facial cues of adiposity. Although this result demonstrates the existence of systematic individual differences in the facial adiposity preferences, it offers little insight into the psychological mechanisms that cause these individual differences. Given previous work linking individual differences in pathogen disgust (i.e., disgust experienced in response to potential sources of pathogens) and both face preferences (e.g., Jones et al., 2013) and attitudes to overweight individuals (e.g., Lieberman et al., 2011), the study reported in the next chapter tested for possible correlations between preferences for facial adiposity and pathogen disgust.

Chapter 3: Individual differences in pathogen disgust predict men's, but not women's, preferences for facial cues of weight

This chapter is based on the following published paper:

Fisher, C. I., Fincher, C. L., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2013). Individual differences in pathogen disgust predict men's, but not women's, preferences for facial cues of weight. *Personality and Individual Differences*, *55*, 860-863.

Abstract

Previous research suggests that people who score higher on measures of pathogen disgust demonstrate (1) stronger preferences for healthy individuals when assessing their facial attractiveness and (2) stronger negative attitudes about obese individuals. The relationship between pathogen disgust and attractiveness judgments of faces differing in cues of weight has yet to be investigated, however. Here we found that men's, but not women's, pathogen disgust was positively correlated with their preference for facial cues of lower weight. Moreover, this effect of pathogen disgust was independent of the possible effects of moral and sexual disgust. These data implicate pathogen disgust in individual differences in preferences for facial cues of weight, at least among men, and suggest that the sex-specific effects of pathogen disgust on preferences for facial cues of weight may be different to those previously reported for general negative attitudes about obese individuals.

Introduction

The importance of pathogens as a selective pressure for the human genome (Fumagalli et al., 2011) is thought to have shaped the evolution of two distinct aspects of the immune system (Fincher & Thornhill, 2012; Schaller, 2006): the classical immune system (i.e., physiological mechanisms of defense against parasites) and the behavioral immune system (i.e., psychology and behaviors for avoiding and managing infectious disease). Given the face's importance for social interaction, responses to facial cues may be an important aspect of the behavioral immune system. Indeed, people who are particularly concerned about infectious disease tend to show stronger aversions to facial cues thought to be associated with poor health (e.g., reduced sex-typical shape characteristics, Thornhill & Gangestad, 2006), particularly when assessing the attractiveness of potential mates (reviewed in Jones et al., 2013b). These studies typically assessed individual differences in concerns about pathogens using the pathogen disgust subscale of the Three Domains of Disgust Scale (TDDS, Tybur et al., 2009). Experimentally priming concerns about pathogens strengthens preferences for putative cues of good health in potential mates (Little et al., 2011c), complementing correlational findings.

Other research into the behavioral immune system has focused on the stigmatization of obese individuals. For example, obese individuals elicit pathogen disgust in post-industrialized societies (Lieberman et al., 2011). Additionally, concerns about infectious disease are positively correlated with the strength of negative attitudes about obese individuals (Park et al., 2007), particularly among women (Lieberman et al., 2011). People can judge others' weight from facial cues and tend to prefer faces displaying cues of relatively low weight (Coetzee et al., 2009). Moreover, rated facial adiposity (the perception of heavier weight in the face) is correlated with measures of poor health, such as shorter lifespan (Reither et al., 2009). Although facial attractiveness is correlated with immune system response in men (Rantala et al., 2012), but not women (Rantala et al., 2013b), rated facial adiposity is correlated with greater frequency of past illness in samples combining men and women (Coetzee et al., 2009) or including women only (Tinlin et al., 2013). Rated facial adiposity is also correlated with inefficient immune system response in men (Rantala et al., 2013a). Together, these findings raise the possibility that individual differences in pathogen disgust predict attractiveness judgments of faces differing in cues of weight.

Here we investigated the relationship between participants' responses on the pathogen, sexual, and moral disgust subscales of the TDDS and their attractiveness judgments of faces differing in cues of weight. Given previous research reporting correlations between face preferences and pathogen disgust (reviewed in Jones et al., 2013), we predicted that (1) participants who scored higher on the pathogen disgust subscale of the TDDS (i.e., participants who showed the greatest concern about infectious disease) would show the strongest aversions to individuals with relatively high levels of facial adiposity and (2) this effect of pathogen disgust would be independent of the possible effects of sexual or moral disgust. Lieberman et al's (2011) finding that women who score high on pathogen disgust hold particularly strong negative attitudes about obese individuals suggests that pathogen disgust may be a particularly good predictor of women’s responses to facial cues of weight. However, Lee et al’s (2013) finding that pathogen disgust more reliably predicts men’s than women’s preferences for putative health cues suggests that pathogen disgust may be a particularly good predictor of men’s responses to facial cues of weight.

Methods

Participants

Sixty-two heterosexual couples (mean relationship duration=18.4 months, SD=15.1) participated in this study as part of an ongoing project investigating the relationship between mate preferences and choices. Other components of this project were unrelated to the current hypotheses and were randomly interspersed among the tests reported here (i.e., were unlikely to have systematically biased responses). Men’s mean age was 21.8 years (SD=1.96) and women’s mean age was 21.2 years (SD=1.94).

Stimuli

Stimuli were full-color images of 50 male (mean age=24.2 years, SD=3.99 years) and 50 female (mean age=24.3 years, SD=4.01 years) faces with neutral expressions and direct gaze. Images were taken under standardized lighting conditions, against a constant background, were standardized on pupil position, and masked so clothing was not visible. Height and weight measurements for these men (mean height=180.2 cm, SD=6.62 cm; mean weight=77.3 kg, SD=12.4 kg) and women (mean height=168.6 cm, SD=6.48 cm; mean weight=57.2 kg, SD=11.4 kg) were used to calculate their body mass index

(BMI; men: M=23.7 kg/m^2, SD=3.13 kg/m^2, range=17.7-31.0 kg/m^2; women: M=20.1 kg/m^2, SD=3.66 kg/m^2, range=16.2-38.4 kg/m^2).

The male faces were rated for weight by 25 raters (15 women, 10 men; mean age=22.54 years, SD=5.05) in a randomized order using a 1 (very underweight) to 7 (very overweight) scale (Cronbach's alpha=.96). A different group of 25 raters (23 women, 2 men; mean age=24.11 years, SD=6.94) rated the female faces for weight using the same method (Cronbach's alpha=.95). Average adiposity ratings for each face (male: M=3.83, SD=0.82; female: M=3.65, SD=0.88) were positively correlated with BMI (men: r=.58, N=50, p<.001; women: r=.66, N=50, p<.001).

Procedure

Participants in our main study rated the attractiveness of the 50 male and 50 female faces using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. Inter-rater agreement for these ratings was high (Cronbach's alphas for men rating women, men rating men, women rating women, and women rating men were all > 0.90). Participants also completed the TDDS (Table 1). Responses on the three TDDS subscales were scored following Tybur et al. (2009). Higher scores represent greater disgust sensitivity. The TDDS and face ratings were completed in a fully randomized order. Male and female faces were presented in separate, randomly ordered blocks of trials in the face-rating task, and, within each block, trial order was fully randomized. The order of TDDS items was also fully randomized in the questionnaire block. As in previous research (Tybur et al., 2011), women reported greater sexual

($t(61)=7.10$, $p<.001$, $d=0.90$) and pathogen ($t(61)=2.20$, $p=.032$, $d=0.28$) disgust than men. Women and men did not differ significantly in moral disgust ($t(61)=-0.23$, $p=.82$, $d=0.03$). Partners' scores for sexual disgust were positively correlated ($r=.38$, $N=62$, $p=.002$), but partners' scores for pathogen ($r=-.01$, $N=62$, $p=.95$) and moral ($r<.01$, $N=62$, $p>.99$) disgust were not.

Results

For each participant, we first calculated the correlation between (1) their attractiveness rating for each of the 50 men's faces and those 50 men's rated facial adiposity (mean $r=-.14$, $SD=.14$), (2) their attractiveness rating for each of the 50 men's faces and those 50 men's BMI (mean $r=-.09$, $SD=.14$), (3) their attractiveness rating for each of the 50 women's faces and those 50 women's rated facial adiposity (mean $r=-.19$, $SD=.13$), and (4) their attractiveness rating for each of the 50 women's faces and those 50 women's BMI (mean $r=-.24$, $SD=.12$). Note that this procedure produces four correlation coefficients for each participant (representing their preferences for perceived adiposity in male faces, cues of BMI in male faces, perceived adiposity in female faces, and cues of BMI in female faces, respectively). These preference scores (i.e., correlation coefficients) served as the dependent variables in subsequent analyses. For each of these preference scores, larger positive values indicate stronger preferences for facial cues of heavier weight and larger negative values indicate stronger preferences for facial cues of lower weight.

In order to establish whether preferences for rated adiposity and preferences for cues of BMI measure similar constructs, we analyzed men's and women's preference scores for own-sex and opposite-sex faces using factor analysis. Analysis of women's preferences for perceived adiposity and cues of BMI in opposite-sex faces produced a single factor (labeled *women's preference for cues of weight in men's faces*) that explained 88% of the variance in women's preference scores and was highly correlated with both of the original variables (both r=.94). A corresponding analysis of women's judgments of own-sex faces also produced a single factor (labeled *women's preference for cues of weight in women's faces*) that explained 83% of the variance in women's preference scores and was highly correlated with both of the original variables (both r=.91). Similar factor analyses were conducted for men's face preferences. Analysis of men's preferences for perceived adiposity and cues of BMI in opposite-sex faces produced a single factor (labeled *men's preference for cues of weight in women's faces*) that explained 86% of the variance in men's preference scores and was highly correlated with both of the original variables (both r=.93). A corresponding analysis of men's judgments of own-sex faces also produced a single factor (labeled *men's preference for cues of weight in men's faces*) that explained 86% of the variance in men's preference scores and was highly correlated with both of the original variables (both r=.93). These preference scores were used in our main analyses. Higher scores indicate stronger preferences for facial characteristics associated with heavier weight.

To test for main effects of TDDS subscales and possible interactions between TDDS subscales and sex of face judged, responses were analyzed using ANCOVAs. Women's preferences for cues of weight in men's and women's faces were analyzed first. *Sex of face judged* (male, female) was a within-subject factor and *pathogen disgust*, *sexual disgust*, and *moral disgust* were entered simultaneously as covariates. This analysis revealed no significant effects (all $F<1.33$, all $p>.25$, all partial $eta^2<.023$). However, a corresponding analysis for men's preferences revealed significant effects of *pathogen disgust* ($F(1,58)=5.99$, $p=.017$, partial $eta^2=.094$) and *moral disgust* ($F(1,58)=5.73$, $p=.020$, partial $eta^2=.090$). There were no other significant effects (all $F<1.28$, all $p>.26$, all partial $eta^2<.021$).

To interpret the main effects of *pathogen disgust* and *moral disgust* on men's preferences we conducted a regression analysis, in which the average of *men's preference for cues of weight in women's faces* and *men's preference for cues of weight in men's faces* was entered as the dependent variable and *pathogen disgust* and *moral disgust* were entered simultaneously as predictors. This analysis revealed a significant negative relationship between *pathogen disgust* and men's preference for cues of weight ($t=-2.52$, standardized beta=-.35, $p=.014$) and a significant positive relationship between *moral disgust* and men's preference for cues of weight ($t=2.43$, standardized beta=.34, $p=.018$). Including sexual disgust as an additional predictor in this regression analysis did not alter the pattern of results.

An additional, custom model ANCOVA that included data from both male and female participants revealed a significant interaction between *participant sex* (male, female) and *pathogen disgust* ($F(1,116)=5.96$, $p=.016$, partial $eta^2=.049$), confirming that pathogen disgust had different effects on men's and women's face preferences. The interactions between *participant sex* and *sexual disgust* and *moral disgust* were not significant, however (all $F<1.60$, all $p>.20$, all partial $eta^2<.015$).

Discussion

Men with higher pathogen disgust showed stronger preferences for facial cues of lower weight, complementing other recent research suggesting pathogen disgust predicts men's responses to facial cues of health (e.g., Jones et al., 2013; Lee et al., 2013). The effect of pathogen disgust on men's face preferences was independent of possible effects of moral and sexual disgust, revealing a domain-specific effect of disgust sensitivity on preferences for facial cues of weight. Although previous work found that pathogen disgust was a particularly good predictor of women's responses to obese individuals (Lieberman et al., 2011), pathogen disgust did not predict women's facial attractiveness judgments in our study. That pathogen disgust here predicted men's, but not women's, preferences for cues of weight is consistent with Lee et al's (2013) finding that pathogen disgust may be a more reliable predictor of men's than women's preferences for putative health cues. Further research is needed to establish why (and when) this sex-specific pattern of results may emerge.

The different patterns of results in our and Lieberman et al's (2011) studies could reflect differences in the nature of the attitudes to heavier individuals that were assessed. While Lieberman et al. (2011) examined participants' responses on questionnaires assessing individual differences in general social attitudes to obese individuals, our study examined attractiveness judgments of face photographs. Although other methodological differences may also contribute to the different patterns of results observed in our and Lieberman et al's studies, the different patterns suggest that pathogen disgust may have somewhat different effects on general social attitudes and face preferences. If this were the case, it would complement other recent work suggesting that ratings of facial attractiveness and perceptions of general social regard are not necessarily synonymous (e.g., Sutherland et al., 2013).

Although it was not an *a priori* prediction of our study, men who scored higher on moral disgust showed weaker preferences for cues of low weight. Moreover, this effect of moral disgust was independent of the observed effect of pathogen disgust on men's face preferences. One possible explanation for this unexpected finding is that men who score higher on moral disgust generally hold weaker appearance-based stereotypes. Further work is needed to explore this possibility.

We found that men, but not women, who scored higher on pathogen disgust showed stronger aversions to faces displaying cues of heavier weight (i.e., individuals displaying higher levels of facial adiposity). This result complements other recent research linking pathogen disgust to face preferences (reviewed in Jones et al., 2013) and implicates pathogen disgust in individual differences in preferences for facial cues of weight, at least among men. Although other studies also suggest that pathogen disgust may be a particularly reliable predictor of men's preferences for facial cues of health (Lee et al., 2013), the sex-specificity of our findings is somewhat surprising, given Lieberman et al's

(2011) work suggesting that pathogen disgust is a particularly good predictor of women's negative attitudes towards obese individuals. Nonetheless, together, these findings suggest that the sex-specific effects of pathogen disgust on preferences for facial cues of weight may be different to those that occur for general negative attitudes about obese individuals.

Whereas Chapter 2 reported an association between partner BMI and own preferences for facial adiposity, revealing individual differences in adiposity preferences, the current chapter investigated pathogen disgust as a potential source of individual differences in facial adiposity preferences. While there was evidence that pathogen disgust may play a role in men's preferences for facial cues of adiposity, pathogen disgust appeared to be unrelated to women's preferences for facial cues of adiposity. Consequently, it is unlikely that pathogen disgust alone can explain the individual differences in preferences for facial cues of adiposity that was observed in Chapter 2.

Previous research on preferences for facial cues of adiposity has either experimentally manipulated face shape cues associated with measures of adiposity or tested for correlations between ratings of unmanipulated face images and those individuals' BMIs. However, because low levels of adiposity can come about through two main routes (good health, on one hand, and illness, on the other hand) people may integrate information from shape cues of adiposity with information from other health cues when judging the attractiveness and health of faces. The next chapter investigated this possibility by testing for interactions between shape cues of adiposity and color cues when judging facial health and attractiveness.

Chapter 4: Integrating shape cues of adiposity and color information when judging facial health and attractiveness

This chapter is based on the following published paper:

Fisher, C. I., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2014). Integrating shape cues of adiposity and color information when judging facial health and attractiveness. *Perception*, *43*, 499-508.

Abstract

Facial cues of adiposity play an important role in social perceptions, such as health and attractiveness judgments. Although relatively low levels of adiposity are generally associated with good health, low levels of adiposity are also a symptom of many communicable diseases. Consequently, it may be important to distinguish between individuals displaying low levels of facial adiposity because they are in good physical condition and those displaying low levels of facial adiposity because they are ill. Integrating information from facial cues of adiposity with information from other health cues, such as facial coloration, may facilitate such distinctions. Here, participants rated the health and attractiveness of face images experimentally manipulated to vary in shape cues of adiposity and color cues associated with perceived health. As we had predicted, the extent to which faces with low levels of adiposity were rated more positively than faces with relatively high levels of adiposity was greater for faces with healthy color cues than it was for faces with unhealthy color cues. Such interactions highlight the integrative processes that allow us to distinguish

between healthy and unhealthy individuals during social interactions, potentially reducing the likelihood of contracting infectious diseases.

Introduction

Many recent findings suggest that facial cues of adiposity are an important factor in human mate preferences. For example, male and female faces perceived as having relatively low levels of adiposity (i.e., levels slightly lower than the population average) tend to be perceived as healthy and attractive (Coetzee et al., 2009; Rantala et al., 2013a, 2013b). Additionally, ratings of men's and women's facial adiposity are negatively correlated with objective measures of their physical health (Coetzee et al., 2009), their reported frequency and/or duration of past health problems (Coetzee et al., 2009; Tinlin et al., 2013), and their longevity (Reither et al., 2009). Facial cues of adiposity are also negatively correlated with the efficiency of men's hepatitis B antibody response (Rantala et al., 2013a) and women's average (i.e., trait) hormone levels (Tinlin et al., 2013). Men and women in romantic relationships with individuals who have a higher body mass index (BMI) also show weaker preferences for faces displaying cues of low levels of adiposity (see Chapter 2). This finding potentially implicates preferences for facial cues of adiposity in men's and women's actual mate choices.

Consistent with research showing that ratings of facial adiposity and BMI are positively correlated (Coetzee et al., 2009; Tinlin et al., 2013; see also Chapter 2), these findings for relationships between facial cues of adiposity and attractiveness, perceived health, and partner characteristics are similar to those that have been reported in research that investigated body cues of BMI (Courtiol et al., 2010; Crossley et al., 2012; Rantala et al., 2013a; Tovee et al., 1998, 1999; Yanover & Thompson, 2010). Similarly, the findings for facial cues of adiposity and health measures described above complement those that have been reported in research investigating the relationship between BMI and health measures (Adams et al., 2014; Berrington de Gonzalez et al., 2010; Guh et al., 2009).

Although relatively low levels of facial adiposity are associated with good long-term health (Coetzee et al., 2009; Reither et al., 2009; Tinlin et al., 2013), low levels of adiposity are also a symptom of many communicable diseases, such as gastroenteritis (Glass et al., 2009; Kahan et al., 2011) and malaria (Girard et al., 2007). This raises the potentially important question of how people can distinguish individuals who have low levels of adiposity because they are in good physical condition from individuals who have low levels of adiposity because they are ill. One way to distinguish between these two groups of individuals might be to integrate information from cues of adiposity with information from other potential health cues, such as facial coloration. In other words, people may use information from health cues like facial coloration to clarify whether individuals displaying low levels of adiposity do so because they are in good physical condition or because they are ill. Indeed, recent research suggests that aspects of facial coloration function as cues of physical condition. For example, increasing redness, yellowness, and, to a lesser extent, lightness in male and female face images increases perceptions of health (Stephen et al., 2009a, 2009b, 2011), while other studies suggest that redness and yellowness are associated with cardiovascular health and good diet, respectively (Stephen et al., 2009b, 2011; Whitehead et al., 2012). Many models of non-human animals' mate preferences incorporate interactions between the effects of cues to different aspects of physical condition (Candolin, 2003). Such interactions may increase the reliability with which individuals can assess others' condition (Candolin, 2003). Few studies of mating-related perceptions in humans have tested for such interactions, however.

In light of the above, we investigated whether people integrate information from cues of adiposity and coloration when assessing the health and attractiveness of men's and women's faces. We did this by assessing perceptions of experimentally manipulated shape cues of adiposity in faces that had healthy coloration in one condition and unhealthy coloration in another condition. If people do use color cues in faces to disambiguate whether individuals displaying low levels of adiposity do so because they are in good physical condition or because they are ill, the extent to which faces with lower levels of adiposity are rated more positively (i.e., perceived to be healthier and more attractive) than faces with higher levels of adiposity would be greater for faces with healthy color cues than for faces with unhealthy color cues.

Methods

Participants

Two hundred and thirty-eight heterosexual women (mean age = 23.15 years, SD = 5.67 years) and 142 heterosexual men (mean age=26.06 years, SD=5.84 years) participated in this online study. Previous research has demonstrated that online and laboratory studies of face shape (DeBruine et al., 2007) and face color (Lefevre et al., 2013) preferences produce very similar patterns of results.

Stimuli

Face stimuli were manufactured to represent all possible combinations of the factors *color dimension* (two levels: red versus yellow), *color value* (two levels: increased versus decreased), and *facial adiposity* (two levels: increased versus decreased). Example stimuli are shown in Figure 1.

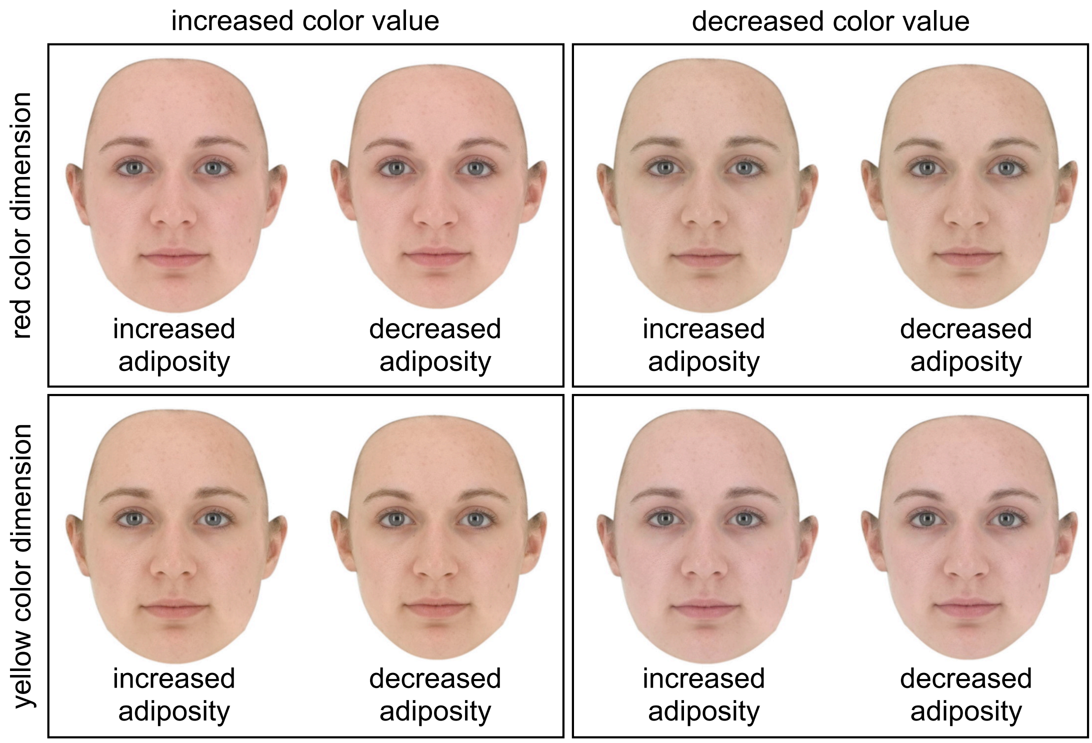

Figure 1. An example of a composite female face that has been manipulated to possess all possible combinations of the factors *color dimension* (red, yellow), *color value* (increased, decreased), and *facial adiposity* (increased, decreased).

To manufacture the face stimuli, we first created 10 unique composite male faces and 10 unique composite female faces (following Re & Perrett, 2014). Each of these composite faces was made by averaging the shape, color, and texture information from color-calibrated (Hong et al., 2001) face images of three different individuals. Male composites were created by averaging male face images and female composites were created by averaging female face images. The computer graphic methods used to average the shape, color, and texture information are detailed in Tiddeman et al. (2001) and have been used to manufacture stimuli in many other previous face perception studies (e.g., Burriss et al., 2009; Jones et al., 2005; Moore et al., 2011; Re & Perrett, 2014). The methods we used for color calibrating face images are detailed in Stephen et al. (2009a) and have been used to color calibrate images in many other previous face perception studies (e.g., Stephen et al., 2011; Whitehead et al., 2012). The individuals photographed were white students at the University of St Andrews.

Next, we independently manipulated these composite face images' redness and yellowness in CIELab color space (CIE, 1976). CIELab color space is modeled on the human visual system and consists of three independent color axes: red (a*), yellow (b*), and lightness (L*). Using methods described in Stephen et al. (2009a), we created two versions of each composite face: one in which red was increased by three units and one in which red was decreased by three units. Again using methods described in Stephen et al. (2009a), we created two additional versions of each composite face: one in which yellow was increased by three units and one in which yellow was decreased by three units.

Importantly, these red and yellow manipulations only affect the manipulated color dimension (i.e., altering redness does not affect yellowness, and vice versa) and do not affect shape information (Stephen et al., 2009a). This technique for manipulating color information in faces has also been used in many other previous studies (e.g., Stephen et al., 2011; Whitehead et al., 2012). We manipulated faces in red and yellow, but not lightness, because the effects of lightness on health perceptions are weaker than those of red and yellow, particularly for male faces (Stephen et al., 2009a). Note that faces were manipulated in either red or yellow, not both red and yellow. These color manipulations, in which color values were increased or decreased by 3 units, are within the normal range of coloration for white adult faces (Whitehead et al., 2012).

We then manipulated shape cues of adiposity in each of the four color-manipulated versions of the composite faces (i.e., we manipulated shape cues in the versions of the composites with increased red, decreased red, increased yellow, decreased yellow). This shape manipulation was carried out by adding (to increase perceived adiposity) or subtracting (to decrease perceived adiposity) 50% of the linear differences in 2D shape between prototypes with the average facial shape information of the 10 individuals with the highest BMI (males: mean=28.39 kg/m^2, SD=1.61 kg/m^2; females: mean=24.81 kg/m^2, SD=5.95 kg/m^2) and the 10 individuals with the lowest BMI (males: mean=19.95 kg/m^2, SD=1.08 kg/m^2; females: mean=17.24 kg/m^2, SD=0.45 kg/m^2) in the images used in Chapter 2 to each of the color-manipulated composite faces. Male prototypes defined the continuum used to manipulate cues of adiposity in the male face images and female prototypes defined the continuum used to manipulate cues of adiposity in the female face images. Details of the computer graphic methods used for these linear shape manipulations are described in Tiddeman et al. (2001). Importantly, manipulating shape cues using this method does not alter the color or texture information of the face images. Consistent with other studies (Coetzee et al., 2009; Tinlin et al., 2013), perceived facial adiposity and measured BMI are highly correlated in the sample of images from which the high and low BMI prototypes were manufactured (see Chapter 2). The method we used to manipulate shape cues of adiposity in faces is similar to that used in previous work assessing the effects of cues of adiposity on perceptions of faces (Re & Perrett, 2014).

Finally, the color-manipulated and shape-manipulated composite face images were standardized on pupil position and masked so that hairstyle and clothing were not visible. In total, these shape and color manipulations produced eight separate versions of each of the 10 male and 10 female base faces, yielding 80 male and 80 female face images in total (see Figure 1 for examples).

Procedure

The male and female face images described in our *Stimuli* section were presented in separate blocks of trials. Health and attractiveness ratings were also made in separate blocks of trials. Participants were randomly allocated to rate *either* the health *or* attractiveness of *either* the male *or* female faces using 1 (very low) to 7 (very high) scales. Each participant was allocated to only one condition. In each condition, the 80 faces were presented individually remaining onscreen until the participant entered their rating. Trial order was randomized for each participant. This method for assessing the attractiveness and perceived health of face images has been used in many previous studies (e.g., Jones et al., 2001; Moore et al., 2013, Tigue et al., 2012). One hundred and ninety-three participants rated the female faces and 187 participants rated the male faces.

Analyses

Inter-rater agreement for ratings of men's and women's faces was high for both attractiveness (both Cronbach's alphas > .93) and health (both Cronbach's alphas > .86) judgments. Consequently, we calculated the mean attractiveness and health ratings for each face. These mean scores were initially calculated separately for men's and women's ratings. However, because an initial analysis showed that the predicted interaction between *color value* (increased, decreased) and *facial adiposity* (increased, decreased) was not qualified by any higher order interactions involving the within-item factor *rater sex* (male, female), we collapsed ratings across the variable *rater sex* and did not include *rater sex* in the main analysis reported below.

Ratings were analyzed using a mixed-design ANOVA with the within-item factors *judgment type* (attractiveness, health), *color dimension* (red, yellow), *color value* (increased, decreased), and *facial adiposity* (increased, decreased), and the between-items factor *sex of face* (male, female). All interactions were tested. Note that this analysis treats items, rather than subjects, as the main unit of analysis. We employed this type of analysis, in which items, rather than raters, served as our main unit of analysis, to address concerns that interactions between the effects of different manipulated facial characteristics may not necessarily generalize across items (Boothroyd et al., 2009). *Judgment type* (attractiveness, health) was included as a factor in the ANOVA so that we could directly compare the effects of the image manipulations on health and attractiveness judgments.

Results

The ANOVA showed significant main effects of *judgment type* (F (1,18) = 156.89, p < .001, η_p^2 = .90), *facial adiposity* (F (1,18) = 138.57, p < .001, η_p^2 = .89), and *color value* (F (1,18) = 527.40, p < .001, η_p^2 = .97). The main effect of *judgment type* indicated that faces received significantly higher ratings for health judgments (M = 3.85, *Standard Error of the Mean* = 0.05) than attractiveness judgments (M = 3.20, *SEM* = 0.08). The main effect of *facial adiposity* indicated that faces with lower levels of adiposity received significantly higher ratings (M = 3.76, *SEM* = 0.07) than faces with higher levels of adiposity (M = 3.29, *SEM* = 0.06). The main effect of *color value* indicated that faces with increased color values received higher ratings (M = 3.64, *SEM* = 0.07) than faces with decreased color values (M = 3.41, *SEM* = 0.06). Neither the main effect of *color dimension* (F (1,18) = 1.19, p = .29, η_p^2 = .06) nor the main effect of *sex of face* (F (1,18) = 0.86, p = .37, η_p^2 = .05) was significant.

Supporting our key prediction that color values would modulate the extent to which facial adiposity influenced ratings, the interaction between *facial adiposity* and *color value* was significant (F (1,18) = 9.60, p = .006, η_p^2 = .35, Figure 2). As we had predicted, the extent to which faces with lower levels of adiposity

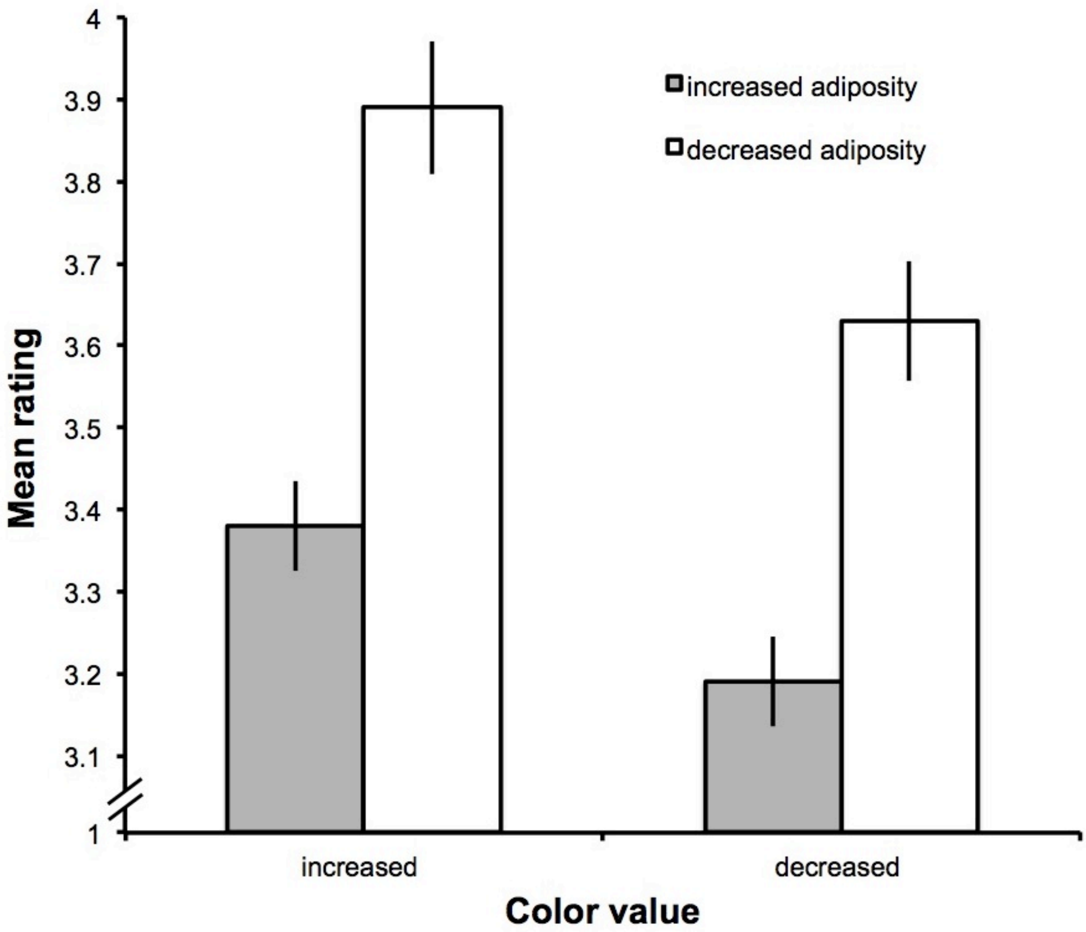

Figure 2. The significant interaction between *facial adiposity* and *color value*. The effect of adiposity was greater when rating faces with increased color values than when rating faces with decreased color values. Bars show means and SEM.

were rated more positively than faces with higher levels of adiposity was greater for faces with increased color values ($t(19) = 10.17$, $p < .001$, mean difference = 0.51, SE mean difference = 0.05) than for faces with decreased color values ($t(19) = 9.24$, $p < .001$, mean difference = 0.44, SE mean difference = 0.05). A three-way interaction among *facial adiposity*, *color value*, and *judgment type* approached significance ($F\ (1,18) = 3.51$, $p = .077$, $\eta_p^2 = .16$), suggesting that the effect of *color value* on the extent to which faces with lower levels of adiposity were rated more positively than faces with higher levels of adiposity may have tended to be greater for health than attractiveness judgments. No other three-way or higher-order interactions involving both *facial adiposity* and *color value* qualified the interaction between *facial adiposity* and *color value* (all F (1,18) < 1.99, all p > .17, all $\eta_p^2 < .10$).

A significant two-way interaction between *facial adiposity* and *face sex* (F (1,18) = 8.30, p = .01, $\eta_p^2 = .32$) reflected *facial adiposity* having a greater effect on ratings of female faces (t(9) = 13.69, p < .001, mean difference = 0.59, SE mean difference = 0.04) than male faces (t(9) = 5.26, p = .001, mean difference = 0.36, SE mean difference = 0.07). A significant two-way interaction between *face sex* and *judgment type* (F (1,18) = 11.38, p = .003, $\eta_p^2 = .39$) reflected female faces tending to be rated as more attractive than male faces (t(18) = 1.78, p = .09, mean difference = 0.29, SE mean difference = 0.16), but not healthier (t(18) = -0.57, p = .58, mean difference = -0.06, SE mean difference = 0.10). A significant two-way interaction between *judgment type* and *facial adiposity* (F (1,18) = 27.69, p < .001, $\eta_p^2 = .61$) reflected *facial adiposity* having a greater effect on attractiveness judgments (t(19) = 10.25, p < .001, mean difference = 0.58, SE mean difference = 0.06) than health judgments (t(19) = 8.20, p < .001, mean difference = 0.37, SE mean difference = 0.05).

There was also a significant interaction between *color dimension* and *color value* (F (1,18) = 4.55, p = .047, $\eta_p^2 = .20$), whereby the effect of *color value* on ratings was greater for faces manipulated in yellow (t(19) = 13.67, p < .001, mean difference = 0.26, SE mean difference = 0.02) than it was for faces manipulated in red ($t(19) = 12.66$, $p < .001$, mean difference = 0.20, SE mean difference = 0.02). There was also a significant interaction between *judgment type* and *color value* (F (1,18) = 235.25, $p < .001$, $\eta_p^2 = .93$), whereby the effect of *color value* was greater for health judgments ($t(19) = 27.43$, $p < .001$, mean difference = 0.38, SE mean difference = 0.01) than it was for attractiveness judgments ($t(19) = 4.79$, $p < .001$, mean difference = 0.07, SE mean difference = 0.01). These two-way interactions were qualified by a three-way interaction among *judgment type*, *color dimension*, and *color value* (F (1,18) = 5.02, p = .038, $\eta_p^2 = .22$), whereby *color value* had significant effects on health ratings of faces manipulated in yellow ($t(19) = 12.61$, $p < .001$, mean difference = 0.39, SE mean difference = 0.03), health ratings of faces manipulated in red ($t(19)$ = 19.19, $p < .001$, mean difference = 0.38, SE mean difference = 0.02), attractiveness ratings of faces manipulated in yellow ($t(19) = 5.67$, $p < .001$, mean difference = 0.13, SE mean difference = 0.02), but not attractiveness ratings of faces manipulated in red ($t(19) = 0.59$, $p = .56$, mean difference = 0.01, SE mean difference = 0.02). A four-way interaction among *face sex*, *judgment type*, *color dimension*, and *color value* approached significance (F (1,18) = 3.75, $p = .069$, $\eta_p^2 = .17$). We did not explore this very high order interaction further because it was not an *a priori* prediction. No other interactions were significant or approached significance (all F (1,18) < 2.99, all p > .10, all $\eta_p^2 < .15$).

Discussion

Consistent with prior work linking facial cues of adiposity to perceptions of attractiveness and health (Coetzee et al., 2009; Rantala et al., 2013a, 2013b;

see also Chapter 2), participants in our study generally gave higher attractiveness and health ratings to faces displaying cues of relatively low levels of adiposity. That this effect of adiposity was greater for perceptual judgments of women than men (Hume & Montgomerie, 2001) and greater for attractiveness judgments than health judgments (Stephen & Perera, 2014; see also Coetzee et al., 2011) is also consistent with previous research. The tendency for cues of adiposity to have stronger effects on attractiveness judgments than health judgments may be due to media portrayals of attractive ideals often possessing levels of adiposity that are lower than is optimal for health appearance (Coetzee et al., 2011; Stephen & Perera, 2014). The tendency for adiposity to have greater effects on perceptions of women than men may reflect a sex difference in the importance of the qualities associated with adiposity (Hume & Montgomerie, 2001), but could also occur because the adiposity manipulations we applied to male and female faces were not necessarily equivalent.

As we had predicted, we also observed a significant interaction between the effects of adiposity and color cues on health and attractiveness ratings; the effect of adiposity was greater for ratings of faces with increased red and yellow color values. Since redness and yellowness in faces are both reliably associated with perceived health (Stephen et al., 2009a, 2009b, 2011), the observed interaction between the effects of adiposity and color cues supports our proposal that people use the additional health information contained in facial color cues to distinguish between individuals displaying facial cues of low levels of adiposity because they are in good physical condition and those displaying facial cues of low levels of adiposity because they are ill. Interactions between the effects of different cues to physical condition have been observed in many non-human species' mate choices and are thought to function to increase the reliability with which individuals can assess others' physical condition (Candolin, 2003). Our results suggest cue integration in human social perception might also function, at least in part, to facilitate more accurate assessments of others' physical condition.

We found that increasing redness and yellowness in faces increased health perceptions. Additionally, increasing yellowness increased facial attractiveness, but increasing redness did not. These results are consistent with previous studies demonstrating that increasing yellowness in faces reliably increases perceived health and attractiveness and increasing redness reliably increases perceived health (Stephen et al., 2009a, 2009b, 2011, 2012a), but that facial redness is not necessarily reliably associated with attractiveness (Stephen et al., 2012a). We speculate that the tendency for individuals displaying red facial cues to be perceived as dominant and aggressive (Stephen et al., 2012a) may counteract the positive effect of redness on health perceptions when people are assessing others' facial attractiveness. While people generally tend to prefer facial cues that increase health perceptions, this is not necessarily true of cues that also increase perceptions of anti-social personality characteristics, such as dominance and aggression (e.g., Fink & Penton-Voak, 2002).

We do not know whether the interaction between the effects of color cues and adiposity on face perceptions that was observed for white faces in the current study would necessarily also occur for perceptions of other ethnicities. Although facial redness and yellowness have similar effects on health perceptions in white European (Stephen et al., 2009a; Stephen et al., 2011) and black African (Stephen et al., 2009b; Stephen et al., 2011) faces, studies also suggest that preferences for adiposity in white European and black African samples may differ (Coetzee et al., 2009, 2012). Coetzee et al. (2009) found that intermediate levels of adiposity were optimally attractive in the white European sample, while Coetzee et al. (2012) found that faces with very low levels of adiposity were considered optimally attractive in the black African sample. These results suggest that it may be useful to compare how people integrate facial shape and color information in different geographic regions. Indeed, integration of information from color cues and shape cues of adiposity may be more apparent in geographic regions where illnesses associated with rapid weight loss are particularly common and the importance of distinguishing between healthy and unhealthy individuals may be greater (see DeBruine et al., 2010, 2011 and Moore et al., 2013 for evidence that pathogen load predicts regional variation in preferences for potential health cues in faces).

In summary, we show a significant interaction between the effects of adiposity and color cues on perceptions of faces; the positive effect of cues of low adiposity levels was greater for ratings of faces with healthy-looking coloration (i.e., increased red and yellow values). We suggest that integrating information from facial color cues and cues of adiposity when assessing others' health and attractiveness may function, at least in part, to increase the accuracy of our perceptions of others' health by making it easier for us to distinguish between individuals displaying facial cues of low levels of adiposity because they are in good physical condition and those displaying facial cues of low levels of adiposity because they are ill. Thus, our results highlight the integrative processes and mechanisms that underpin social perceptions of faces and, potentially, shape social interactions.

The previous chapters reported individual differences in the strength of preferences for facial cues of adiposity (Chapters 2 and 3) and that the strength of preferences for shape cues of adiposity can be modulated by facial color cues (Chapter 4). This latter finding suggests that information from multiple health cues is integrated when judging facial health and attractiveness. Some previous research has suggested that physical attractiveness in women is associated with their openness to short-term sexual relationships (i.e., their sociosexual orientation). Although most work on adiposity cues and attractiveness has focused on adiposity as a health cue, the importance of adiposity cues for physical attractiveness raises the possibility that adiposity may also contain information about women's sociosexual orientation. To investigate this issue, the next chapter investigated the interrelationships among women's sociosexual orientation, BMI, and facial attractiveness. Waist-hip ratio was also considered in this study.

Chapter 5: Is women's sociosexual orientation related to their physical attractiveness?

This chapter is based on the following published paper:

Fisher, C. I., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2016). Is women's sociosexual orientation related to their physical attractiveness? *Personality and Individual Differences*, *101*, 396-399.

Abstract

Although many researchers have suggested that more physically attractive women report less restricted sociosexual orientations (i.e., report being more willing to engage in short-term, uncommitted sexual relationships), evidence for this association is equivocal. Consequently, we tested for possible relationships between women's scores on the revised version of the Sociosexual Orientation Inventory (SOI-R) and women's body mass index (N=212), waist-hip ratio (N=213), ratings of their facial attractiveness (N=226), and a composite attractiveness measure derived from these three intercorrelated measures. Our analyses suggest that more attractive women report less restricted sociosexual orientations. Moreover, we show that this link between attractiveness and sociosexual orientation is not simply a consequence of women's scores on the behavior subscale of the SOI-R. Importantly, however, the correlations between measures of women's physical attractiveness and their reported sociosexual orientation were very weak, suggesting that perceptions of these potential cues of women's sociosexual orientation are unlikely to provide accurate, socially relevant information about others during social interactions.

Introduction

Individual differences in sociosexuality (i.e., the extent to which people are willing to engage in short-term, uncommitted sexual relationships, Simpson & Gangestad, 1991) have been the focus of a considerable amount of empirical research (see Penke & Asendorpf, 2008 and Schmitt, 2005 for reviews). Sociosexuality is most commonly assessed using versions of the Sociosexual Orientation Inventory (SOI), which was first developed by Simpson and Gangestad (1991) and revised (SOI-R) by Penke and Asendorpf (2008). Higher scores on these scales indicate a more unrestricted sexual strategy (i.e., greater openness to short-term, uncommitted sexual relationships).

Many researchers have tested for possible correlations between women's attractiveness and their sociosexual orientation. On one hand, more attractive women might be expected to be more open to short-term relationships because they have more opportunities to mate with high quality mates and, consequently, are better positioned to benefit from a short-term mating strategy (e.g., Gangestad & Simpson, 1990). On the other hand, more attractive women might be expected to have more restricted sociosexual orientations because they can be "choosier" (Penton-Voak et al., 2003).

Evidence for correlations between women's physical attractiveness and sociosexual orientation is mixed, however. Some studies have found that women with more attractive faces scored higher on the Sociosexual Orientation Inventory (Boothroyd et al., 2008, 2011). Women with more attractive body shapes or voices also report having been an extra-pair sexual partner more frequently and having had more extra-pair sexual relationships than do women with relatively unattractive body shapes or voices (Hughes & Gallup Jr, 2003; Hughes et al., 2004). By contrast, other studies have not observed significant correlations between women's facial or body attractiveness and their reported sociosexual orientation (Clark, 2004; Penke & Asendorpf, 2008; Perilloux et al., 2013), their reported number of short-term or extra-pair sexual relationships (Rhodes et al., 2005; Wiederman & Hurst, 1998), or their reported need for emotional closeness in sexual relationships (Weeden & Sabini, 2007). Note, however, that frequency of extra-pair mating will only indicate unrestricted sociosexual orientation for individuals in long-term exclusive relationships. Attractiveness ratings of video clips showing women interacting with a male confederate are also not significantly correlated with their scores on the Sociosexual Orientation Inventory (Stillman & Maner, 2009).

There are several possible reasons for the mixed results outlined above. First, studies of facial attractiveness have not controlled for the effects of makeup on attractiveness ratings (see, e.g., Etcoff et al., 2011), which may obscure or create correlations between sociosexual orientation and facial attractiveness. Second, only two studies of the possible relationship between women's facial attractiveness and sociosexual orientation assessed sociosexual orientation using the SOI-R (Perilloux et al., 2013; Penke & Asendorpf, 2008). Neither of these studies reported significant positive correlations between women's attractiveness and sociosexual orientation. Furthermore, Penke and Asendorpf (2008) reported a weak *negative* correlation between facial attractiveness and scores on the SOI, but not on the SOI-R, suggesting that the scale used to assess sociosexual orientation could be important. Third, studies reporting significant positive correlations between facial attractiveness and SOI (Boothroyd et al., 2008, 2011) used a method in which participants indicated whether a composite face with the average facial shape, color, and texture information of women who scored high on the SOI was more attractive than a composite face with the average facial shape, color, and texture information of women who scored low on the SOI. As Boothroyd et al. (2008) acknowledged, results of such comparisons would not necessarily generalize to ratings of individual faces.

In light of the above, we investigated the relationship between women's facial attractiveness and their scores on Penke and Asendorpf's (2008) revised version of the Sociosexual Orientation Inventory (SOI-R). To control for the effects of makeup on facial attractiveness, facial attractiveness was assessed from third-party ratings of face images of the women taken after they had removed their makeup. We also tested for possible relationships between women's scores on the SOI-R and two body measures known to be negatively correlated with women's attractiveness (reviewed in Weeden & Sabini, 2005): their body mass index (BMI) and waist-hip ratio (WHR). We investigated these issues in the largest sample of women tested to date (Ns= 212 to 226, depending on analysis).

Methods

First, digital face photographs of 226 young adult white women (mean age=20.73 years, SD=2.03 years) were taken. All of these women were students or staff at the University of Glasgow. Each woman first cleaned her face with hypoallergenic face wipes to remove any makeup and was photographed a minimum of 10 minutes later. Photographs were taken in a small windowless room against a constant background and under standardized diffuse lighting conditions. Participants were instructed to pose with a neutral expression. Camera-to-head distance and camera settings were held constant. Participants wore a white smock covering their clothing when photographed. Photographs were taken using a Nikon D300S digital camera and a GretagMacbeth 24-square ColorChecker chart was included in each image for use in color calibration. Following previous research (e.g., Jones et al., 2015), face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to ensure that color values in each image reflected the true color information (Hong et al., 2001). All images were aligned on pupil position and hairstyle and clothing were masked.

Height and weight were measured from 212 of the women (14 women chose not to have their height and/or weight measured) and were used to calculate their BMI (M=23.32 kg/m^2, SD=3.69 kg/m^2). According to the World Health Organization's (WHO) classifications (World Health Organization, 2000), 3% of these women were in the underweight BMI category (<18.5 kg/m^2), 74% were in the normal category (18.5-24.99 kg/m^2), 16% were in the overweight category (≥25 kg/m^2), and 7% were in the obese category (≥30 kg/m^2). None of these women were extremely underweight (i.e., none had BMI < 15 kg/m^2, Bray, 1978) and none had a BMI lower than 17 kg/m^2. Waist and hip circumferences were measured from 213 of the women (13 women chose not to have their waist and/or hip circumference measured) and were used to calculate their WHR (M=0.76, SD=0.06). Age was weakly correlated with WHR (rho=.13, N=213, p=.054) and unrelated to BMI (rho=.10, N=212, p=.15).

All 226 women photographed completed the 5-point response scale version of the revised Sociosexual Orientation Inventory (SOI-R), which has previously been shown to have very good internal, external, and test-retest reliability (Penke & Asendorpf, 2008). The questionnaire consists of 9 items, each of which is answered using a 1 to 5 scale. The SOI-R has three components (behavior, attitudes, and desires). The SOI-R behavior component consists of 3 items (e.g., “With how many different partners have you had sex within the past 12 months?”), for which 1 on the response scale corresponds to “0 sexual partners” and 5 corresponds to “8 or more sexual partners” (M=2.13, SD=0.90). The SOI-R attitudes component consists of 3 items (e.g., “Sex without love is OK”), for which 1 on the response scale corresponds to “totally disagree” and 5 corresponds to “totally agree” (M=3.27, SD=1.15). The SOI-R desires component consists of 3 items (e.g., “In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met?”), for which 1 on the response scale corresponds to “never” and 5 corresponds to “nearly every day” (M=2.67, SD=0.99). Scores for each component are calculated by summing the individual scores for the 3 relevant items. Our mean scores are similar to those reported for female university students by Penke and Asendorpf (2008). A total score (global SOI-R) can also be calculated by summing the three component scores. Higher scores indicate more unrestricted sociosexuality (i.e., greater openness to short-term mating). Following recent work investigating the correlation between women's physical attractiveness and sociosexual orientation that used the SOI-R (Perilloux et al., 2013), our main analyses used these global SOI-R scores. Age was related to scores on the behavior subscale (rho=.18, N=226, p=.006), but not the attitude subscale (rho=.07, N=226, p=.32), desire subscale (rho=.01, N=226, p=.92), or global SOI-R scores (rho=.11, N=226, p=.12).

The face images were rated for attractiveness by 626 heterosexual men (mean age=25.95 years, SD=6.65 years) using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. Each man was randomly allocated 25 of the women's faces to rate. Men's attractiveness ratings of women can differ according to the temporal context of the relationship for which they are being judged (see, e.g., Little et al., 2014). Consequently, 328 of the men were instructed to rate the women's attractiveness for a short-term relationship ("You are looking for the type of person who would be attractive in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship, and possibility of a one-night stand."). The other 298 men were instructed to rate the women's attractiveness for a long-term relationship ("You are looking for the type of person who would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with, and someone you may, at some point, wish to marry or enter into a relationship on similar grounds as marriage"). These definitions of short- and long-term relationships have been used in previous research (e.g., Penton-Voak et al., 2003).

Following Han et al. (2016) and Fruhen et al. (2015), inter-rater reliability for attractiveness ratings was estimated using bootstrapping. This technique computed the average correlation between ratings for each face (derived from randomly selected subsamples of participants over ten thousand iterations) separately for short-term and long-term attractiveness. The average correlation was high for both types of attractiveness rating (both $r>.75$, both $SD<.03$). This bootstrapping procedure was used because each participant had rated only a random subset of the full image set. We then calculated the average attractiveness rating for each face separately for the short-term ($M=2.31$, $SD=0.63$) and long-term ($M=2.37$, $SD=0.60$) contexts. These average ratings were used in our analyses. Younger women tended to be rated as more attractive for both short-term ($rho=-.13$, $N=226$, $p=.05$) and long-term ($rho=-.12$, $N=226$, $p=.06$) contexts.

Results

Not all variables were normally distributed (p-values for Kolmogorov-Smirnov tests ranged from $<.001$ to .26). Consequently, we report results of non-parametric tests. Global SOI-R scores were positively correlated with rated facial attractiveness in both the long-term ($rho=.16$, $N=226$, $p=.018$) and short-term ($rho=.15$, $N=226$, $p=.029$) contexts. Although women with lower BMI or lower WHR tended to have higher global SOI-R scores, these correlations were not significant (BMI: $rho=-.12$, $N=212$, $p=.083$; WHR: $rho=-.11$, $N=213$, $p=.105$).

Facial attractiveness ratings for both the long-term and short-term contexts were negatively correlated with women’s BMI (long-term: rho=-.34, N=212, p<.001; short-term: rho=-.32, N=212, p<.001) and WHR (long-term: rho=-.29, N=213, p<.001; short-term: rho=-.27, N=213, p<.001). Consequently, we subjected women’s facial attractiveness in the long-term context, facial attractiveness in the short-term context, BMI, and WHR to principal component analysis with no rotation. This analysis produced a single “attractiveness” component that explained ~60% of the variance in scores (Kaiser-Meyer-Olkin measure of sampling adequacy=0.62; Bartlett's test of sphericity: p<.001). Scores on this attractiveness component were strongly positively correlated with both types of facial attractiveness rating (both rho>.89, N=212, p<.001) and strongly negatively correlated with both BMI (rho=-.55, N=212, p<.001) and WHR (rho=-.54, N=212, p<.001). Scores on this attractiveness component were positively correlated with global SOI-R scores (rho=.16, N=212, p=.020).

Additional analyses showed qualitatively similar patterns of results when scores on the behavior, attitudes, and desires subscales were substituted for global SOI-R. These results are shown in Table 2.

Table 2. Correlations between aspects of sociosexual orientation (assessed using Penke and Asendorpf's SOI-R) and aspects of women's physical attractiveness. Spearman's rho (and p values) are reported.

	Global SOI-R	Behavior SOI-R	Attitudes SOI-R	Desires SOI-R
Facial attractiveness (long-term)	.16 (.02)	.11 (.09)	.12 (.07)	.13 (.05)
Facial attractiveness (short-term)	.15 (.03)	.10 (.15)	.11 (.09)	.13 (.05)
BMI	-.12 (.08)	-.17 (.01)	-.14 (.04)	.03 (.64)
WHR	-.11 (.11)	-.04 (.60)	-.13 (.07)	-.08 (.23)
Attractiveness component	.16 (.02)	.11 (.10)	.14 (.04)	.10 (.14)

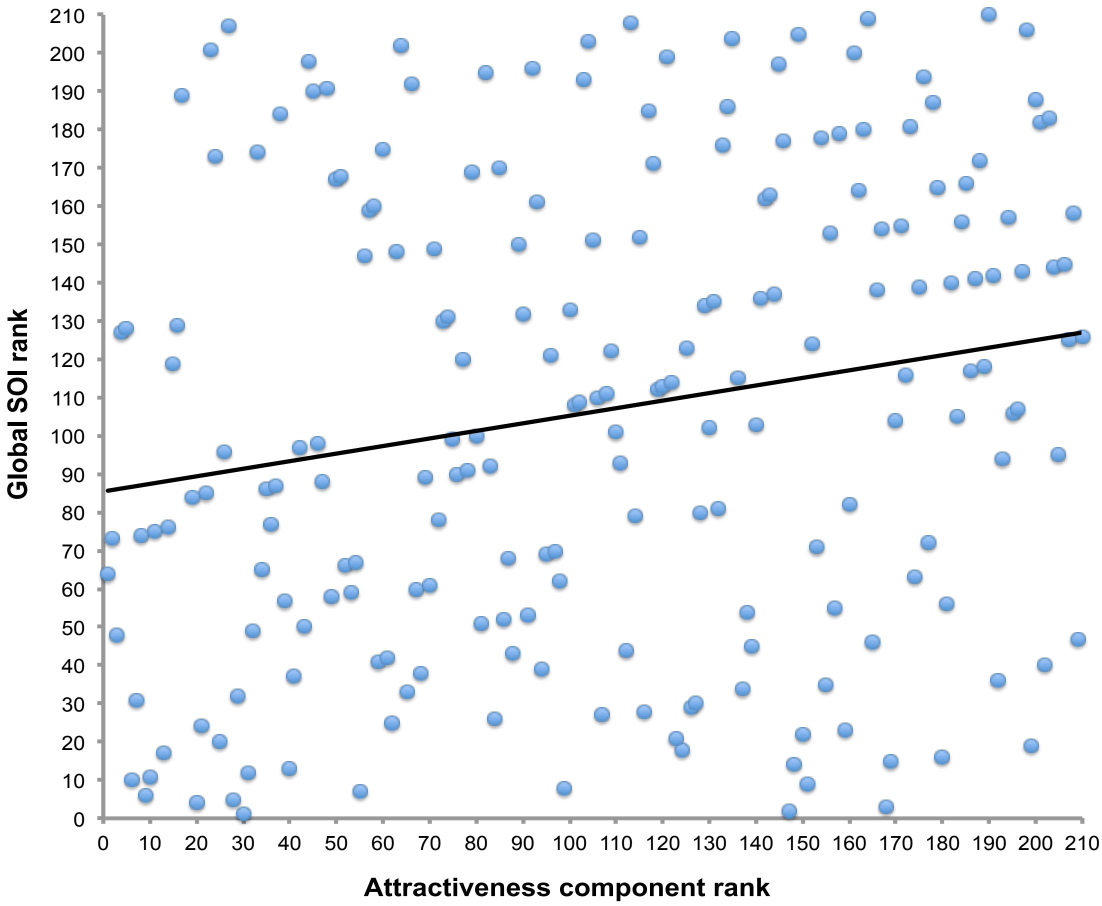

Figure 3. The relationship between women's global SOI-R scores and scores on the attractiveness component.

Discussion

We found that more facially attractive women scored higher on the SOI-R (i.e., reported greater willingness to engage in short-term, uncommitted sexual relationships). This pattern of results was observed when women's faces were rated for attractiveness as either a short-term or long-term partner. We also observed a significant, positive relationship between women's scores on the SOI-R and a composite attractiveness measure derived from principal component analysis of their facial attractiveness ratings, BMI, and WHR. Women with lower BMI or lower WHR also tended to score higher on the SOI-R, although these relationships were not significant (p=.08 and p=.11, respectively). Nonetheless, collectively, our findings are consistent with previous research reporting positive relationships between measures of women's attractiveness and measures of their openness to short-term, uncommitted sexual relationships (Boothroyd et al., 2008, 2011; Hughes & Gallup Jr, 2003; Hughes et al., 2004). We speculate that more attractive women may be more open to short-term sexual relationships because they are better placed to offset the potential costs of engaging in short-term relationships, such as low investment and/or reputational costs.

The relationships between our measures of women's physical attractiveness and their scores on the behavior, desires, and attitudes subscales of the SOI-R were generally very similar to those observed for global SOI-R (see Table 2). This suggests that the tendency for more attractive women to score higher on global SOI-R is unlikely to be driven solely by their actual sexual behavior (i.e., is unlikely to be simply a direct consequence of their responses on the behavior subscale only). Additionally, women were not wearing makeup in the face photographs and images were masked so that hairstyle and clothing were not visible. Consequently, the correlations between women's facial attractiveness and SOI-R observed in the current study cannot be due to makeup, hairstyle, or clothing revealing women's sociosexual orientation. Given previous research has not controlled for the possible effects of makeup on attractiveness, our results are the first to suggest that women's faces contain correlates of their sociosexual orientation that are not due to makeup alone.

Consistent with previous research (e.g., Han et al., 2016; Penton-Voak et al., 2003; see also Chapters 2 - 4), we found that women with lower BMI and lower (i.e., more feminine) WHR had more attractive faces. Given BMI and WHR are both negatively correlated with women's body attractiveness (reviewed in Weeden & Sabini, 2005), our results are also consistent with previous research suggesting that women with more attractive bodies tend to have more attractive faces (e.g., Thornhill & Grammer, 1999). The strength of the relationships between women's body measurements and their facial attractiveness did not differ when women's faces were rated for short-term and long-term relationships (BMI: rho=-.32 versus rho=-.34; WHR: rho=-.27 versus rho=-.29). This pattern of results suggests that men's preferences for femininity or adiposity cues in women's faces do not differ according to the temporal context of the relationship sought (but see Little et al., 2014). Further research would be needed to clarify the possible relationships between sociosexual orientation and other measures of adiposity (e.g., percentage body fat), body shape, and facial appearance (e.g., morphological facial femininity).

Our results demonstrate that more physically attractive women score higher on the SOI-R, suggesting that attractiveness is linked to greater openness to short-term, uncommitted sexual relationships. Moreover, our results suggest that this link between sociosexual orientation and physical attractiveness is unlikely to be simply a direct consequence of more attractive women having more mating opportunities. Importantly, however, the correlations between the measures of physical attractiveness considered in our study and women's SOI-R were uniformly weak (absolute rho values ranging from .11 to .16 for global SOI-R). This suggests that perceptions of these potential cues of women's sociosexual orientation are unlikely to provide accurate, socially relevant information about others during social interactions.

Chapter 6: General Discussion

Summary

Previous research had identified facial adiposity as a potentially important cue to health (Coetzee et al., 2009; Tinlin et al., 2013; Reither et al., 2009) and physical attractiveness (Coetzee et al., 2009, 2012; Han et al., 2016; Rantala et al., 2013a, 2013b). The studies reported in this thesis investigated (i) individual differences in preferences for facial cues of adiposity and whether these preferences are related to actual partner choice, (ii) variation in pathogen disgust as a potential predictor of facial adiposity preferences, (iii) the integration of facial cues of color and adiposity in relation to health and attractiveness judgments, and (iv) the interrelationships among women's sociosexual orientation, facial attractiveness, BMI, and waist-hip ratio.

Although several lines of evidence report assortative mating for adiposity (for a meta-analytic review, see Di Castelnuovo et al., 2009), evidence for assortative *preferences* for cues of adiposity (whereby leaner people show stronger preferences for leaner individuals) was equivocal. Moreover, little was known about whether preferences for facial cues of adiposity are related to actual partner choice. To address this gap in the literature, Chapter 2 examined whether people's preferences for cues of adiposity in opposite-sex faces predict either their own BMI or their partner's BMI. Consistent with previous work reporting a correlation between men's and women's preferences for leaner *body* images and their actual partner's BMI (Courtiol et al., 2010) and work suggesting that face preferences predict romantic partner choice (see, e.g., DeBruine et al., 2012), we found that participants' preferences for facial cues of

BMI in opposite-sex faces predicted their actual partners' BMIs. In other words, people with leaner romantic partners reported stronger preferences for opposite-sex faces displaying cues of low BMI. Although we found evidence of assortative mating for BMI in our sample (romantic partners' BMIs were positively correlated), we found no evidence of assortative preferences for cues of adiposity. That is, own BMI and preferences for cues of BMI in opposite-sex faces were not significantly correlated and independently predicted partner's BMI. Despite preferences for facial cues of BMI explaining some of the variance in the BMI of men's and women's romantic partners, this variance was entirely independent of that which was explained by assortative mating for BMI. These results suggest that individual differences in preferences for facial cues of BMI contribute little (if at all) to assortative mating for BMI. That no significant correlation was observed between own BMI and preferences for facial cues of BMI is consistent with other work reporting no significant correlations between measures of people's own adiposity and their preferences for cues of adiposity in opposite-sex bodies (Price et al., 2013).

Market-value-contingent preferences, whereby physically attractive individuals show stronger preferences for attractive characteristics when assessing potential mates (see e.g., Little & Mannion, 2006), may offer one possible explanation as to why assortative preferences contributed little (if at all) to assortative mating in our sample. Rather than resulting from assortative preferences for cues of adiposity, assortative mating for adiposity is potentially due (at least in part) to individuals with higher levels of adiposity experiencing additional constraints on their mate choices (Speakman et al., 2007; see also

Zietsch et al., 2011). These constraints may arise because the pool of individuals willing to choose romantic partners with higher levels of adiposity is likely to be smaller (and contain a higher proportion of overweight individuals) than the pool of individuals willing to choose relatively lean romantic partners (Speakman et al., 2007). Consistent with this proposal, Bajos et al. (2010) found that individuals with higher levels of adiposity reported having had a lower number of sexual partners in the previous year than relatively lean individuals.

Although the correlation between partner's BMI and preferences for facial cues of adiposity reported in Chapter 2 demonstrates the existence of systematic variation in facial adiposity preferences, little was known about the underlying psychological mechanisms causing these individual differences. Other work has suggested that pathogen disgust (i.e., disgust experienced in response to possible sources of infectious disease) may explain some individual differences in preferences for facial cues of health (e.g., Lee et al., 2013). Consequently, Chapter 3 investigated whether pathogen disgust predicts individual differences in preferences for facial adiposity. We found that men with higher pathogen disgust reported stronger preferences for lower levels of facial adiposity, complementing other recent work linking pathogen disgust to men's preferences for facial cues of health (e.g., Jones et al., 2013a; Lee et al., 2013).

Despite prior work suggesting that pathogen disgust is a particularly good predictor of women's attitudes to overweight individuals (Lieberman et al., 2011), pathogen disgust did not predict women's preferences for facial cues of adiposity in our sample. The contrasting pattern of results observed in our and

Lieberman's (2011) studies may be a consequence of methodological differences; while Lieberman et al. (2011) used questionnaires to assess individual differences in general social attitudes towards obese people, our study examined participants' preferences for facial cues of adiposity. Indeed, it is possible that pathogen disgust affects general social attitudes and face preferences differently. In line with this proposal, Sutherland et al. (2013) reported that perceptions of general social regard and facial attractiveness judgments are not necessarily synonymous. That men's, but not women's, pathogen disgust predicted facial adiposity preferences in our sample is consistent with Lee et al's (2013) sex-specific pattern of results, whereby pathogen disgust more reliably predicted men's than women's preferences for putative health cues. In summary, although Chapter 3 presented evidence that pathogen disgust plays a role in preferences for facial cues of adiposity (at least in men), it is unlikely that the individual differences in facial adiposity preferences observed in Chapter 2 can be explained by pathogen disgust alone.

Given that some models of non-human animals' mate preferences predict interactions between the effects of cues signalling information about physical condition (Candolin, 2003), it is possible that humans also integrate information from different health-related cues in order to increase the reliability with which they can assess the condition of others. Chapter 4 investigated this possibility by examining whether people integrate information from cues of adiposity and skin coloration when judging the health and attractiveness of men's and women's faces. Consistent with previous research suggesting that facial cues of adiposity are linked to perceptions of health and attractiveness (Coetzee et al., 2009; Rantala et al., 2013a, 2013b; see also Chapter 2), faces displaying cues of relatively low levels of adiposity were generally awarded higher health and attractiveness ratings. We also found that skin color values modulated the extent to which facial adiposity influenced health and attractiveness ratings; the effect of adiposity was greater for judgments of faces displaying increased color values than for faces displaying decreased color values. In other words, the extent to which faces with lower levels adiposity were rated more positively than faces with higher levels of adiposity was greater for faces with increased red and yellow color values.

In line with prior research that identified facial redness and yellowness as reliable predictors of perceived health (Stephen et al., 2009a, 2009b, 2011), we found that increasing facial redness and yellowness increased perceptions of health. Taken alongside these results and the results discussed above, the significant interaction we observed between the effects of adiposity and color cues suggests that people integrate these cues in order to improve the accuracy with which they can assess others' physical condition. Although several studies have linked relatively low levels of facial adiposity to good long-term health (Coetzee et al., 2009; Reither et al., 2009; Tinlin et al., 2013), low levels of adiposity may also result from infectious diseases, such as gastroenteritis (Glass et al., 2009; Kahan et al., 2011). Thus, our finding suggests that people use additional health information contained in facial color cues to determine whether individuals displaying facial cues of low levels of adiposity do so because they are in good physical condition or because they are ill.

In addition to finding that skin redness and yellowness were both related to health perceptions in our sample, we also found that faces displaying increased yellowness (but not redness) received higher attractiveness ratings. These results complement other work showing that facial yellowness is reliably associated with health and attractiveness judgements and facial redness is reliably associated with health judgements (Stephen et al., 2009a, 2009b, 2011, 2012a), but that facial redness is not necessarily a reliable predictor of attractiveness judgements (Stephen et al., 2012a). Given that facial redness has been linked to perceptions of dominance and aggression (Stephen et al., 2012a), it is possible that an association between facial redness and anti-social personality traits can dampen the effect of redness on facial attractiveness.

While Chapters 2 and 3 reported variation in the strength of participants' preferences for facial cues of adiposity, Chapter 4 reported evidence of facial color cues modulating the strength of these preferences for shape cues of adiposity. This latter finding suggests that people integrate information from multiple facial cues when assessing the health and attractiveness of others. Additionally, we found that the effect of adiposity reported in Chapter 4 (i.e., general preference for lower levels of facial adiposity) was greater for perceptual judgments of women than men and greater for attractiveness ratings than health ratings, complimenting the work of Hume and Montgomerie (2001) and Stephen and Perera (2014), respectively.

Previous research on facial adiposity has emphasized facial cues of adiposity's potentially important role as a health cue in social perception and interaction. However, given that adiposity influences facial attractiveness (Coetzee et al., 2009; Hume & Montgomerie, 2001) and physical attractiveness is thought to be linked to women's sociosexual orientation (Boothroyd et al., 2008, 2011), it is also possible that facial cues of adiposity contain information about women's sociosexual orientation. Chapter 5 investigated this possibility by investigating possible interrelationships among women's sociosexual orientation, BMI, waist-hip ratio, and facial attractiveness. We found that women who were rated as more facially attractive for both short- and long-term relationships scored higher on the SOI-R (i.e., reported greater openness to short-term, uncommitted sexual relationships). Moreover, women's scores on the SOI-R were significantly and positively related to a composite attractiveness measure derived from principal component analysis of their facial attractiveness ratings, BMI, and WHR. Our findings complement earlier research reporting positive correlations between measures of women's physical attractiveness and measures of their willingness to engage in short-term, uncommitted sexual relationships (Boothroyd et al., 2008, 2011; Hughes & Gallup, 2003; Hughes et al., 2004).

That facial attractiveness was positively correlated with women's openness to short-term, uncommitted sexual relationships in our sample is consistent with the idea that more attractive women could be better positioned to benefit from a short-term mating strategy because they will have more opportunities to mate with high-quality partners (e.g., Gangestad & Simpson, 1990). Importantly, however, that we observed qualitatively similar patterns of results for scores on the attitudes, behavior, and desires SOI-R subscales suggests that the positive correlation between physical attractiveness and sociosexual orientation is unlikely to be simply a consequence of women's responses on the behavior subscale alone. Further work is needed to identify specifically which facial characteristics are associated with sociosexuality, although the correlation seen here with the composite score derived from both facial attractiveness and body adiposity measures is consistent with the idea that facial correlates of adiposity are one such cue. It should also be noted that the correlations between women's SOI-R scores and measures of physical attractiveness were uniformly weak, suggesting that they are unlikely to be strong enough to influence the behavior of others during social interactions.

Limitations and future directions

BMI is a measure of weight scaled for height and does not directly measure fat mass. Because there are two routes to high BMI (being overweight versus being muscular), some researchers have suggested that alternative indices of adiposity, such as percentage body fat, are more reliable than BMI (see, e.g., Wellens et al., 1996). To further investigate this issue, I ran analyses on a pre-existing dataset from our lab containing BMI (calculated from height and weight measurements) and percentage body fat (calculated using bioelectrical impedance analysis). Results revealed that BMI and percentage body fat were highly correlated in this sample of young white women ($r = .82$) and men ($r = .78$). Given that the sample characteristics (young adult women) are similar to those from which the stimuli were manufactured in my empirical chapters, it may not necessarily be problematic to use BMI to estimate women's adiposity in this type of empirical context. Moreover, other research suggests that BMI generally corresponds well with percentage body fat within age- and sex-specific groups and can reliably distinguish between categories of percentage body fat (see, e.g., Flegal et al., 2009). Nonetheless, we acknowledge that other measures may give a more accurate estimate of women's adiposity.

Our analyses of the relationship between attractiveness and BMI focused on tests for linear relationships. This was partly due to the methods used to estimate individual subjects' preferences for facial cues of BMI, partly due to the techniques used to experimentally manipulate BMI-cues in face images, and partly because only a very small proportion (if any) of the images in our studies came from people with unhealthily low BMIs. Some research on women's attractiveness and BMI has reported curvilinear relationships, in which the correlation between BMI and attractiveness is weaker for relatively slim women (e.g., Coetzee et al., 2009; Rantala et al., 2013b). However, other studies have not replicated this pattern of results (Han et al., 2016). The rationale for predicting curvilinear relationships is that the optimal BMI for health and fertility in women is closer to 'average' than it is to 'low' (Wang et al., 2015). However, cross-cultural research on judgments of women's physical attractiveness has shown that optimally attractive BMIs are substantially lower than those that are optimal for health and fertility (Wang et al., 2015). Nonetheless, we acknowledge that the relationship between attractiveness and adiposity may be more complex than the linear relationships demonstrated in this thesis.

Interestingly, it has recently been shown that facial cues of adiposity might be a better predictor of health than traditional measures of obesity such as BMI and percentage body fat. Research suggests that certain aspects of health (e.g., duration and frequency of respiratory infections) are more strongly related to facial adiposity than to BMI (Coetzee et al., 2009). Furthermore, Tinlin et al. (2013) found that perceived facial adiposity contains health-related information over and above that which is explained by BMI (i.e., rated facial adiposity predicted health status even when controlling for BMI). Other work has shown that diseases such as diabetes type II are better identified by neck adiposity (measured using a lipometer) than by BMI, percentage body fat, or measurements of adipose tissue at 14 other body locations inferior to the neck (Möller et al., 2000). By contrast, that rated facial adiposity appears to be unrelated to immune function and oxidative stress suggests that these components of health may be less clearly related to facial adiposity (Foo et al., 2017). Future research could build on these contrasting findings within the literature by examining facial adiposity's relationship to multiple aspects of health, including health biomarkers that have not yet been studied in relation to facial adiposity (e.g., telomere length, which is a good predictor of healthy aging and longevity, Atzmon et al., 2010).

Another interesting avenue for future studies would be examining how within- and between-subject adiposity changes influence social perceptions of faces. My recent involvement in a collaborative project led by Dr James McLaren (Institute of Cardiovascular and Medical Sciences, University of Glasgow) is creating a dataset to investigate this issue. This longitudinal study tracked weight gain and loss in White and South Asian male participants over 12 weeks using measures of adiposity and cardiovascular health (e.g., adipose biopsies and metabolic testing). Face photographs of participants were taken at each stage of their weight change journey. We will examine the effects of within- and between-subject changes in adiposity on aspects of facial appearance, such as skin coloration and perceived health and attractiveness. Future work could also model the effects of within-person weight change on facial appearance and test whether this can motivate healthier behaviors, such as exercise and healthy eating. Modelling the effects of eating fruit and vegetables on facial appearance has previously been shown to improve fruit and vegetable consumption in young adults (Whitehead et al., 2011). Such interventions could be particularly useful for motivating healthy behavior in young adults, who are a group that might value short-term effects on appearance over longer-term effects on health outcomes.

Given that my empirical chapters examined primarily White European participants' judgements of White European face images, the results reported in this thesis do not necessarily translate to other cultures. Recent studies investigating the degree of cross-cultural similarity in face preferences have typically focused on preferences for facial coloration in different cultures. Stephen et al. (2012b) found that skin yellowness, redness, and lightness, were positively correlated with women's attractiveness ratings of men's faces in a Black African sample. They also found that skin yellowness, but not redness or lightness, was positively correlated with women's attractiveness ratings of men's faces in a White European sample. Coetzee et al. (2014) observed similar coloration preferences among White European participants judging the attractiveness of White faces and Black African participants judging the attractiveness of Black faces, whereby skin yellowness and lightness in women's faces were positively correlated with attractiveness judgments in both samples. With regard to health perceptions, some work suggests that skin redness and yellowness have similar effects on the perceived health of white European (Stephen et al., 2009a; Stephen et al., 2011) and Black African (Stephen et al., 2009b; Stephen et al., 2011) faces. Although these results were interpreted as evidence for cross-cultural similarity in skin color preferences (particularly for facial yellowness), results from recent work in our lab suggest that preferences for facial skin coloration are not universal. While skin yellowness had a positive effect on facial attractiveness ratings among White UK participants, we found that yellowness had a negative effect on facial attractiveness ratings among Chinese participants (Han et al., in preparation). This cultural difference could reflect the tendency for fruit and vegetable consumption to be positively correlated with socioeconomic status in most developed countries, but for vegetable consumption to be negatively correlated with socioeconomic status in China (Wang, 2001).

In keeping with evidence for cross-cultural differences in preferences for facial coloration, research examining cross-cultural differences in preferences for facial adiposity suggests that facial adiposity preferences are not universal. While intermediate levels of adiposity were perceived as optimally attractive in Coetzee et al's (2009) white European sample, low levels of adiposity were perceived as optimally attractive in Coetzee et al's (2012) Black African sample.

In light of these results and those reported in Chapter 4, comparing how people integrate information from facial cues of adiposity and color in different geographic regions may be a fruitful avenue for future research. Indeed, the importance of integrating information from shape and color cues may be greater in geographic regions where the prevalence of diseases associated with rapid weight loss (e.g., malaria) is higher. In such regions, the ability to distinguish between individuals displaying low levels of adiposity because they are healthy or because they are ill would be particularly valuable in facilitating pathogen avoidance. Since pathogen load has previously been shown to predict regional variation in preferences for putative health cues in faces (DeBruine et al., 2010, 2011; Moore et al., 2013; Scott et al., 2014), future work could investigate whether regional variation in pathogen load mediates the interaction between the effects of facial color and adiposity on attractiveness judgments.

The lack of universality in adiposity preferences highlighted by the above findings raises the question of how adiposity preferences initially emerge. Sociocultural theory proposes that the media's portrayal of the 'ideal' body shape encourages people to internalize unrealistic beauty ideals, engage in appearance comparisons with them, and strive to achieve the unattainable, ultimately leading to body dissatisfaction (Stice, 1994; Thompson et al., 1999). The relationship between media exposure and body dissatisfaction among women has been supported by extensive correlational and experimental studies (see Grabe et al., 2008, and Want, 2009, for meta-analyses).

The media's role in shaping body self-image may go some way towards explaining general adiposity preferences, and offers a potential explanation for the finding that adiposity has stronger effects on attractiveness judgments than health judgments (Coetzee et al., 2011; Stephen & Perera, 2014; see also Chapter 4). Indeed, research suggests that physical beauty ideals can be manipulated by visual exposure to altered stimuli (bodies: Boothroyd et al., 2012; Re et al., 2011b; Winkler & Rhodes, 2007; faces: Bestelmeyer et al., 2008; Rhodes et al., 2003b), by classical conditioning and social learning (Jones et al., 2007b), and by the context in which these ideals are presented (Bateson et al., 2014). Re et al. (2011b) found that visual exposure to heavy bodies produced aftereffects on facial adiposity preferences, whereby participants' preferences shifted toward significantly higher facial adiposity following adaptation to heavy bodies.

Interestingly, Boothroyd et al. (2016) found significant differences in preferences for female BMI between Nicaraguan samples varying in their degree of media exposure (measured by amount of television consumption) and Westernization (measured by dieting behavior and acculturation). While the highest BMI preferences were observed in the rural sample with least media access, the lowest BMI preferences were observed in the urban sample where television consumption was highest. Future research could build upon this cross-sectional study by tracking people's preferences for facial cues of adiposity over several years and, ideally, across different cultures (i.e., track the adiposity preferences of migrants).

Relatedly, examining the developmental trajectory of preferences for facial cues of adiposity could be another interesting direction for future research. Several studies have found that children exhibit adult-like responses to faces. From around age 4 to 5, children show agreement with adults about which faces are attractive (Boothroyd et al., 2014; Cavior & Lombardi, 1973; Kissler & Bäuml, 2000). Preferences for facial cues of health seem to emerge from around age 6 to 8 (Boothroyd et al., 2014), followed by facial averageness and symmetry preferences from around age 9 (Boothroyd et al., 2014; Saxton et al., 2009; Saxton et al., 2011). Some researchers have proposed that the new motivation to find a romantic partner brought on by adolescence results in facial attractiveness judgments becoming more fine-tuned and consistent at this stage of development (see e.g., Scherf et al., 2012). Nevertheless, Saxton et al. (2006) found that children, adolescents, and adults were significantly concordant in their ratings of facial attractiveness, suggesting that attractiveness judgments are relatively stable across age groups. By contrast, preferences for facial health appear to increase from late childhood to early adolescence, at least among girls (Boothroyd et al., 2014). In light of research reporting a relationship between adolescents' body dissatisfaction and their ratings of peers' physical attractiveness (Rosenblum & Lewis, 1999), it is possible that self-perception of body image during adolescence plays a crucial role in the developmental trajectory of adiposity preferences. Future work could examine whether activities known to negatively impact body image, such as social media use (see Holland & Tiggemann, 2016, for a review), have long-lasting effects on people's adiposity preferences and whether there is a critical age at which such activities maximally influence preferences.

Several lines of research have examined the relationship between steroid hormones and adiposity. In women, oestrogen level is negatively related to waist-hip ratio (Jasienska et al., 2004) and testosterone level is positively related to central obesity (Bohler et al., 2010). In men, on the other hand, central obesity is typically associated with low testosterone levels in both cross-sectional (Pasquali et al., 1991) and longitudinal (Gapstur et al., 2002; Khaw & Barrett-Connor, 1992) studies. Research examining the link between sex hormones and facial cues of adiposity has reported negative correlations between women's facial adiposity and progesterone levels (Tinlin et al., 2013). The negative relationship between oestrogen and women's facial adiposity reported by Tinlin et al. (2013) did not reach significance, however.

Other work has examined possible relationships between women's facial appearance and cortisol levels. While Rantala et al. (2013b) found that cortisol was significantly correlated with women's facial attractiveness, other work observed no significant relationship between women's cortisol and facial attractiveness (Gonzalez-Santoyo et al., 2015; Han et al., 2016). Furthermore, neither Han et al. (2016) nor Rantala et al. (2013b) observed significant correlations between cortisol and measures of women's adiposity (facial adiposity, BMI, and percentage body fat). In men, however, strong relationships have been documented between cortisol and various body measurements, including BMI, WHR, and sagittal abdominal diameter (see Bjorntorp, 2001 for a review). Further investigation may be required to establish whether there are hormonal correlates of facial adiposity and what they might be.

As an important determinant of physical attractiveness, it is possible that an individual's body shape is advertised through other modalities such as dance. Dance is typically characterised by sex-specific body movements (Hanna, 2010) with certain movements being particularly good predictors of dance quality (Neave et al., 2010). Research suggests that dance attractiveness plays an important role in mating behavior (see Fink et al., 2015 for a review). Indeed, several studies have documented a link between dance attractiveness and physical strength, an important aspect of men's mate quality (see e.g., Sell et al., 2009). While physical strength is positively correlated with dance attractiveness in men (Hugill et al., 2009; McCarty et al., 2013; Weege et al., 2015), it appears to be unrelated to dance attractiveness in women (Weege et al., 2015). Interestingly, Weege et al. (2015) found that BMI did not predict dance attractiveness in either sex, although it should be noted that men's and women's BMIs were log transformed in Weege et al.'s study due to the detection of outliers. In view of work demonstrating that the amplitude of movements is particularly important in signalling dance quality (Neave et al., 2010) and other work showing that higher adiposity is associated with restricted movement (Visser et al., 1998), further investigation of the relationship between dance attractiveness and adiposity could shed light on adiposity's role in dance perception.

Another modality through which information about an individual's body shape might be communicated is the voice. The human voice has been shown to reliably communicate information about several physical attributes, including the speaker's attractiveness, dominance, and body size (see Feinberg, 2008, and

Pisanski et al., 2014, for reviews). A recent meta-analysis by Pisanski et al. (2014) reported that estimates of vocal tract length explained up to 10% of the variance in height and weight within sexes. By contrast, fundamental frequency (i.e., pitch) explained less than 2% of the variance and correlated only weakly with height and weight within sexes (Pisanski et al., 2014).

Despite the wealth of evidence examining the voice’s relationship to height and weight, very few studies have examined the voice’s relationship to adiposity. There is, however, some evidence suggesting that these two dimensions are related. With regard to vocal tract anatomy, Busetto et al. (2009) found that upper airway size (assessed by acoustic pharyngometry) was negatively related to BMI in women. Other work has demonstrated that weight loss is associated with decreased volume of pharyngeal adipose tissue (Shelton et al., 1993). Pisanski et al. (2015) found that estimates of women’s vocal tract length were positively correlated with BMI and negatively correlated with WHR. No significant relationships were observed between estimates of men’s vocal tract length and BMI, however. Although fundamental frequency was significantly and negatively associated with women’s BMI, no significant relationship was observed between fundamental frequency and women’s WHR (Pisanski et al., 2015). While this latter finding complements research suggesting that fundamental frequency is a relatively poor predictor of body shape (Bruckert et al., 2006; Collins 2000), other work has reported a significant negative correlation between fundamental frequency and factor scores obtained from principal component analysis including women’s BMIs, WHRs, and percentage body fat (Vuckovic et al., 2010). One possible explanation for Vuckovic et al.’s

(2010) finding is that women with relatively low levels of oestrogens and/or high levels of androgens might develop both more masculine bodies (i.e., lower WHRs and increased visceral fat, Blouin et al., 2008) in addition to more masculine voices (i.e., lower fundamental frequency, Abitbol et al., 1999). Indeed, the relationship between adiposity and the voice may be further complicated by the fact that androgens and oestrogens appear to affect both vocal characteristics (Bruckert et al., 2006; Busetto et al., 2009; Evans et al., 2008) and regional fat distribution (Bohler et al., 2010). Given that the accuracy at which people can estimate the body shape of others based on vocal traits alone has not yet been investigated, future work could examine which vocal traits people use when estimating the adiposity of others based on their voices.

Conclusion

Facial adiposity is reliably associated with perceptions of attractiveness and health, as well as multiple measures of actual health. Very few studies have investigated the factors that predict systematic variation in preferences for facial cues of adiposity or how such variation is related to social outcomes, however. This thesis demonstrated that individual differences in preferences for facial cues of adiposity predict partner choice and pathogen disgust, revealing possible pathways through which sexual selection and selective pressures might have shaped facial adiposity preferences. That people integrate information from skin color and shape cues of adiposity when judging others' health and attractiveness suggests that responses to facial cues of adiposity function to distinguish between healthy and unhealthy individuals. Adiposity may also communicate information about sexual strategy, although the weak relationship between facial correlates of BMI and women's sociosexual orientation suggests that perceptions of these potential cues of women's sexual strategy are unlikely to play an important role in social interactions.

References

Abitbol, J., Abitbol, P., & Abitbol, B. (1999). Sex hormones and the female voice. *Journal of Voice*, *13*(3), 424-446. doi: 10.1016/S0892-1997(99)80048-4

Adams, K. F., Leitzmann, M. F., Ballard-Barbash, R., Albanes, D., Harris, T. B., Hollenbeck, A., & Kipnis, V. (2014). Body mass and weight change in adults in relation to mortality risk. *American Journal of Epidemiology, 179(2)*, 135-144. doi: 10.1093/aje/kwt254

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, *32*(3), 537-551. doi: 10.1016/S0896-6273(01)00491-3

Alley, T. R., & Cunningham, M. R. (1991). Averaged faces are attractive, but very attractive faces are not average. *Psychological Science*, *2*(2), 123-125. doi: 10.1111/j.1467-9280.1991.tb00113.x

Andreoni, J., & Petrie, R. (2008). Beauty, gender and stereotypes: Evidence from laboratory experiments. *Journal of Economic Psychology*, *29*(1), 73-93. doi: 10.1016/j.joep.2007.07.008

Apicella, C. L., Little, A. C., & Marlowe, F. W. (2007). Facial averageness and attractiveness in an isolated population of hunter-gatherers. *Perception*, *36*(12), 1813-1820. doi: 10.1068/p5601

Armstrong, J. (2004). *The Secret Power of Beauty: Why Happiness is in the Eye of the Beholder*. London: Allen Lane.

Atzmon, G., Cho, M., Cawthon, R. M., Budagov, T., Katz, M., Yang, X., . . . Wright, W. E. (2010). Genetic variation in human telomerase is associated with telomere length in Ashkenazi centenarians. *Proceedings of the*

National Academy of Sciences, 107(Suppl. 1), 1710-1717. doi: 10.1073/pnas.0906191106

Bajos, N., Wellings, K., Laborde, C., & Moreau, C. (2010). Sexuality and obesity, a gender perspective: Results from French national random probability survey of sexual behaviors. *British Medical Journal, 340,* c2573. doi: 10.1136/bmj.c2573

Banducci S. A., Karp J. A., Thrasher M., Rallings C. (2008). Ballot photographs as cues in low-information elections. *Political Psychology, 29*, 903–917. doi: 10.1111/j.1467-9221.2008.00672.x

Bardin, C. W., & Catterall, J. F. (1981). Testosterone: A major determinant of extragenital sexual dimorphism. *Science*, *211*(4488), 1285-1294.

Batres, C., & Perrett, D. I. (2017). How the harsh environment of an army training camp changes human (homo sapiens) facial preferences. *Ethology*, *123*(1), 61-68. doi: 10.1111/eth.12571

Bateson, M., Tovee, M. J., George, H. R., Gouws, A., & Cornelissen, P. L. (2014). Humans are not fooled by size illusions in attractiveness judgements. *Evolution & Human Behavior, 35*, 133–139. doi: 10.1016/j.evolhumbehav.2013.11.007

Bendich, A. (1991). β-Carotene and the immune response. *Proceedings of the Nutrition Society*, *50*, 263-274.

Berggren, N., Jordahl, H., & Poutvaara, P. (2010). The looks of a winner: Beauty and electoral success. *Journal of Public Economics*, *94*(1), 8-15. doi: 10.1016/j.jpubeco.2009.11.002

Berri, D. J., Simmons, R., Van Gilder, J., & O'Neill, L. (2011). What does it mean to find the face of the franchise? Physical attractiveness and the evaluation of athletic performance. *Economics Letters*, *111*(3), 200-202. doi: 10.1016/j.econlet.2011.02.018

Berrington de Gonzalez, A., Hartge, P., Cerhan, J. R., Flint, A. J., Hannan, L, MacInnis, R. J., … Thun, M. J. (2010). Body-mass index and mortality among 1.46 million white adults. *New England Journal of Medicine, 363*, 2211-2219.

Berry, D. S. (2000). Attractiveness, attraction, and sexual selection: Evolutionary perspectives on the form and function of physical attractiveness. *Advances in Experimental Social Psychology*, *32*, 273-342. doi: 10.1016/S0065-2601(00)80007-6

Berry, D. S., & Brownlow, S. (1989). Were the physiognomists right? Personality correlates of facial babyishness. *Personality and Social Psychology Bulletin*, *15*(2), 266-279.

Berscheid, E., & Walster, E. (1974). Physical attractiveness. *Advances in Experimental Social Psychology*, *7*, 157-215.

Bestelmeyer, P. E. G., Jones, B. C., DeBruine, L. M., Little, A. C., Perrett, D. I., Schneider, A., . . . Conway, C. A. (2008). Sex-contingent face aftereffects depend on perceptual category rather than structural encoding. *Cognition, 107(1)*, 353–365. doi: 10.1016/j.cognition.2007.07.018

Bleske-Rechek, A., Kolb, C. M., Stern, A. S., Quigley, K., & Nelson, L. A. (2014). Face and body: Independent predictors of women’s attractiveness. *Archives of sexual behavior*, *43(7)*, 1355-1365. doi: 10.1007/s10508-014-0304-4

Blouin, K., Boivin, A., & Tchernof, A. (2008). Androgens and body fat distribution. *The Journal of Steroid Biochemistry and Molecular Biology*, *108*, 272–280. doi: 10.1016/j.jsbmb.2007.09.001

Bohler, H., Jr., Mokshagundam, S., & Winters, S. J. (2010). Adipose tissue and reproduction in women. *Fertility and Sterility, 94*(3), 795–825. doi: 10.1016/j.fertnstert.2009.03.079

Boothroyd, L. G., Cross, C. P., Gray, A. W., Coombes, C., & Gregson-Curtis, K. (2011). Perceiving the facial correlates of sociosexuality: Further evidence. *Personality and Individual Differences*, *50*, 422-425. doi:

10.1016/j.paid.2010.10.017

Boothroyd, L. G., Jones, B. C., Burt, D. M., Cornwell, R. E., Little, A. C., Tiddeman, B. P., & Perrett, D. I. (2005). Facial masculinity is related to perceived age but not perceived health. *Evolution and Human Behavior*, *26*(5), 417-431. doi: 10.1016/j.evolhumbehav.2005.01.001

Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., & Perrett, D. I. (2008). Facial correlates of sociosexuality. *Evolution and Human Behavior*, *29(3)*, 211-218. doi: 10.1016/j.evolhumbehav.2007.12.009

Boothroyd, L. G., Jucker, J. L., Thornborrow, T., Jamieson, M. A., Burt, D. M., Barton, R. A., . . . Tovee, M. J. (2016). Television exposure predicts body size ideals in rural Nicaragua. *British Journal of Psychology*, 1-16. doi: 10.1111/bjop.12184

Boothroyd, L. G., Lawson, J. F., & Burt, D. M. (2009). Testing immuncompetence explanations of male facial masculinity. *Journal of Evolutionary Psychology, 7(1)*, 65-81. doi: 10.1556/JEP.7.2009.1.7

Boothroyd, L. G., Meins, E., Vukovic, J., & Burt, D. M. (2014). Developmental changes in children's facial preferences. *Evolution and Human Behavior, 35(5)*, 376–383. doi: 10.1016/j.evolhumbehav.2014.05.002

Boothroyd, L. G., Scott, I., Gray, A., Coombes, C., & Pound, N. (2013). Male facial masculinity as a cue to health outcomes. *Evolutionary Psychology, 11*, 1044-1058.

Boothroyd, L. G., Tovee, M. J., & Pollet, T. V. (2012). Visual diet versus associative learning as mechanisms of change in body size preferences. *PLoS One, 7(11)*, e48691. doi: 10.1371/journal.pone.0048691

Bray, G. (1978). Definition, measurement, and classification of the syndromes of obesity. *International Journal of Obesity, 2,* 99-112.

Brown, N. R., & Sinclair, R. C. (1999). Estimating number of lifetime sexual partners: Men and women do it differently. *The Journal of Sex Research, 36,* 292-297. doi: 10.1080/00224499909551999

Bruckert, L., Liénard, J. S., Lacroix, A., Kreutzer, M., & Leboucher, G. (2006). Women use voice parameters to assess men's characteristics. *Proceedings of the Royal Society Biological Sciences Series B, 273*, 83-89. doi: 10.1098/rspb.2005.3265

Budesheim, T. L., & DePaola, S. J. (1994). Beauty or the beast? The effects of appearance, personality, and issue information on evaluations of political candidates. *Personality and Social Psychology Bulletin*, *20*(4), 339-348.

Burriss, R. P., Rowland, H. M., & Little, A. C. (2009). Facial scarring enhances men's attractiveness for short-term relationships. *Personality and Individual Differences, 46*, 213-217. doi: 10.1016/j.paid.2008.09.029

Busetto, L., Mazza, M., De Stefano, F., Costa, G., Negrin, V., & Enzi, G. (2009). Upper airway size is related to obesity and body fat distribution in women. *European Archives of Oto-Rhino-Laryngology*, *266(4)*, 559-563. doi: 10.1007/s00405-008-0773-y

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews, 78,* 575-595. doi: 10.1017/S1464793103006158

Carrington, M., Nelson, G. W., Martin, M. P., Kissner, T., Vlahov, D., Goedert, J. J., . . . O'Brien, S. J. (1999). HLA and HIV-1: Heterozygote advantage and B* 35-Cw* 04 disadvantage. *Science*, *283*(5408), 1748-1752.

Cash, T. F., & Kilcullen, R. N. (1985). The aye of the beholder: Susceptibility to sexism and beautyism in the evaluation of managerial applicants. *Journal of Applied Social Psychology, 15*, 591–605. doi: 10.1111/j.1559-1816.1985.tb00903.x

Cavior, N., & Lombardi, D. A. (1973). Developmental aspects of judgment of physical attractiveness in children. *Developmental Psychology, 8(1)*, 67–71. doi: 10.1037/h0033824

Chiu, R. K., & Babcock, R. D. (2002). The relative importance of facial attractiveness and gender in Hong Kong selection decisions. *International Journal of Human Resource Management*, *13*(1), 141-155. doi: 10.1080/09585190110092857

Clark, A. P. (2004). Self-perceived attractiveness and masculinization predict women's sociosexuality. *Evolution and Human Behavior*, *25(2)*, 113-124. doi: 10.1016/S1090-5138(03)00085-0

Coetzee, V., Barrett, L., Greeff, J. M., Henzi, S. P., Perrett, D. I., & Wadee, A. A. (2007). Common HLA alleles associated with health, but not with facial attractiveness. *PLoS One*, *2*(7), e640. doi: 10.1371/journal.pone.0000640

Coetzee, V., Chen, J., Perrett, D. I., & Stephen, I. D. (2010). Deciphering faces: Quantifiable visual cues to weight. *Perception, 39*, 51–61. doi: 10.1068/p6560

Coetzee, V., Faerber, S. J., Greeff, J. M., Lefevre, C. E., Re, D. E., & Perrett, D. I. (2012). African perceptions of female attractiveness. *PLoS ONE, 7*, e48116. doi: 10.1371/journal.pone.0048116

Coetzee, V., Greeff, J. M., Stephen, I. D., & Perrett, D. I. (2014). Cross-cultural agreement in facial attractiveness preferences: The role of ethnicity and gender. *PLoS ONE, 9*, e99629. doi: 10.1371/journal.pone.0099629

Coetzee, V., Perrett, D. I., & Stephen, I. D. (2009). Facial adiposity: A cue to health? *Perception, 38,* 1700-1711. doi: 10.1068/p6423

Coetzee, V., Re, D., Perrett, D. I., Tiddeman, B. P., & Xiao, D. (2011). Judging the health and attractiveness of female faces: Is the most attractive level of facial adiposity also considered the healthiest? *Body Image, 8,* 190-193. doi: 10.1016/j.bodyim.2010.12.003

Collins, S. A. (2000). Men's voices and women's choices. *Animal Behaviour*, *60*(6), 773–780. doi: 10.1006/anbe.2000.152

Commission Internationale de L'Éclairage. (1976). *CIE Colorimetry – Part 4: 1976 L*a*b* Color Space.* Available: http://www.cie.co.at/index.php/Publications/index.php?i_ca_id=485. Accessed April 12, 2017.

Confer, J. C., Perilloux, C., & Buss, D. M. (2010). More than just a pretty face: Men's priority shifts towards bodily attractiveness in short-term versus long-term mating contexts. *Evolution and Human Behavior, 31,* 348-353. doi: 10.1016/j.evolhumbehav.2010.04.002

Courtiol, A., Picq, S., Godelle, B., Raymond, M., & Ferdy, J.-B. (2010). From preferred to actual mate characteristics: The case of human body shape. *PLoS ONE, 5,* e13010. doi: 10.1371/journal.pone.0013010

Crossley, K. L., Cornelissen, P. L., & Tovee, M. J. (2012). What is an attractive body? Using an interactive 3D program to create the ideal body for you and your partner. *PLoS One, 7*, e50601. doi: 10.1371/journal.pone.0050601

Cunningham, M. R. (1986). Measuring the physical in physical attractiveness: Quasi-experiments on the sociobiology of female facial beauty. *Journal of Personality and Social Psychology*, *50*(5), 925. doi: 10.1037/0022-3514.50.5.925

Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, *59*(1), 61-72. doi: 10.1037/0022-3514.59.1.61

Currie, T. E., & Little, A. C. (2009). The relative importance of the face and body in judgments of human physical attractiveness. *Evolution and Human Behavior, 30,* 409-416. doi: 10.1016/j.evolhumbehav.2009.06.005

Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.

DeBruine, L. M., Fincher, C. L., Watkins, C. D., Little, A. C., & Jones, B. C. (2012). Preference versus Choice: Do face preferences predict actual partner choice? Human Behavior and Evolution Society Conference in Albuquerque, New Mexico.

DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., . . . Tiddeman, B. P. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society of London B: Biological Sciences*, *273(1592)*, 1355-1360. doi: 10.1098/rspb.2005.3445

DeBruine, L. M., Jones, B. C., Little, A. C., Crawford, J. R., & Welling, L. L. M. (2011). Further evidence for regional variation in women's masculinity preferences. *Proceedings of the Royal Society of London B, 278*, 813-814. doi: 10.1098/rspb.2010.2200

DeBruine, L. M., Jones, B. C., Smith, F. G., & Little, A. C. (2010). Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(3), 751-758. doi: 10.1037/a0016457

DeBruine, L. M., Jones, B. C., Unger, L., Little, A. C., & Feinberg, D. R. (2007). Dissociating averageness and attractiveness: Attractive faces are not always average. *Journal of Experimental Psychology: Human Perception and Performance, 33(6)*, 1420–1430. doi: 10.1037/0096-1523.33.6.1420

Di Castelnuovo, A., Quacquaruccio, G., Donati, M. B., De Gaetano, G., & Iacoviello, L. (2009). Spousal concordance for major coronary risk factors: A systematic review and meta-analysis. *American Journal of Epidemiology, 169(1),* 1-8. doi: 10.1093/aje/kwn234

Dion, K., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology*, *24*, 285–290.

Eagly, A. H., Ashmore, R. D., Makhijani, M. G., & Longo, L. C. (1991). What is beautiful is good: A meta-analytic review of research on the physical attractiveness stereotype. *Psychological bulletin*, *110*(1), 109-128.

Elder, G. H. (1969). Appearance and education in marriage mobility. *American Sociological Review, 34*, 519–533. doi: 10.2307/2091961

Enlow, D. H. (1990). Facial Growth (3rd ed.). Philadelphia: Harcourt Brace.

Etcoff, N. (1999). *Survival of the Prettiest: The Science of Beauty*. New York: Anchor/Doubleday.

Etcoff, N. L., Stock, S., Haley, L. E., Vickery, S. A., & House, D. M. (2011). Cosmetics as a feature of the extended human phenotype: Modulation of the perception of biologically important facial signals. *PLoS ONE, 6,* e25656. doi: 10.1371/journal.pone.0025656

Evans, S., Neave, N., Wakelin, D., & Hamilton, C. (2008). The relationship between testosterone and vocal frequencies in human males. *Physiology & Behavior*, *93*, 783–788. doi: 10.1016/j.physbeh.2007.11.033

Feinberg, D. R. (2008). Are human faces and voices ornaments signalling common underlying cues to mate value? *Evolutionary Anthropology: Issues, News, and Reviews*, *17(2)*, 112-118. doi: 10.1002/evan.20166

Feingold A. 1990. Gender differences in effects of physical attractiveness on romantic attraction: A comparison across five research paradigms. *Journal of Personality and Social Psychology, 59(5)*, 981–993. doi: 10.1037/0022-3514.59.5.981

Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: the cases of strong family ties and heightened religiosity. *Behavioral and Brain Sciences, 35*, 61–79. doi: 10.1017/S0140525X11000021

Fink, B., Bunse, L., Matts, P. J., & D’Emiliano, D. (2012). Visible skin colouration predicts perception of male facial age, health and attractiveness. *International Journal of Cosmetic Science*, *34(4)*, 307-310. doi: 10.1111/j.1468-2494.2012.00724.x

Fink, B., Grammer, K., & Matts, P. J. (2006b). Visible skin color distribution plays a role in the perception of age, attractiveness, and health in female faces. *Evolution and Human Behavior*, *27(6)*, 433-442. doi: 10.1016/j.evolhumbehav.2006.08.007

Fink, B., Neave, N., Manning, J. T., & Grammer, K. (2006a). Facial symmetry and judgements of attractiveness, health and personality. *Personality and Individual Differences*, *41*(3), 491-499. doi: 10.1016/j.paid.2006.01.017

Fink, B., & Penton-Voak, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science, 11*, 154-158. doi: 10.1111/1467-8721.00190

Fink, B., Weege, B., Neave, N., Pham, M. N., & Shackelford, T. K. (2015). Integrating body movement into attractiveness research. *Frontiers in psychology*, *6*, 220. doi: 10.3389/fpsyg.2015.00220

Flegal, K. M., Shepherd, J. A., Looker, A. C., Graubard, B. I., Borrud, L. G., Ogden, C. L., . . . Schenker, N. (2009). Comparisons of percentage body fat, body mass index, waist circumference, and waist-stature ratio in adults. *The American journal of clinical nutrition*, *89(2)*, 500-508. doi: 10.3945/ajcn.2008.26847

Fletcher, J. M. (2009). Beauty vs. brains: Early labor market outcomes of high school graduates. *Economics Letters*, *105(3)*, 321-325. doi: 10.1016/j.econlet.2009.09.006

Foo, Y. Z., Simmons, L. W., & Rhodes, G. (2017). Predictors of facial attractiveness and health in humans. *Scientific Reports*, *7*, 39731. doi: 10.1038/srep39731

Fraccaro, P. J., Feinberg, D. R., DeBruine, L. M., Little, A. C., Watkins, C. D., &

Jones, B. C. (2010). Correlated male preferences for femininity in female faces and voices. *Evolutionary Psychology*, *8(3)*, 447-461. doi: 10.1177/147470491000800311

Frisard, M., & Ravussin, E. (2006). Energy metabolism and oxidative stress. *Endocrine*, *29(1)*, 27-32. doi: 10.1385/ENDO:29:1:27

Fruhen, L. S., Watkins, C. D., & Jones, B. C. (2015). Perceptions of facial dominance, trustworthiness and attractiveness predict managerial pay awards in experimental tasks. *The Leadership Quarterly*, *26*, 1005-1016. doi: 10.1016/j.leaqua.2015.07.001

Fumagalli M, Sironi M, Pozzoli U, Ferrer-Admetlla A, Pattini L & Nielsen R (2011). Signatures of environmental genetic adaptation pinpoint pathogens as the main selective pressure through human evolution. *PLoS Genetics, 7*, e1002355. doi: 10.1371/journal.pgen.1002355

Galton, F. J. (1878). Composite portraits. *Nature, 18*, 97 – 100.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and sociobiology*, *14(2)*, 89-96. doi: 10.1016/0162-3095(93)90009-7

Gangestad, S. W., & Simpson, J. A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality*, *58(1)*, 69-96. doi: 10.1111/j.1467-6494.1990.tb00908.x

Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society of London B, 275,* 991-1000. doi: 10.1098/rspb.2007.1425

Gapstur, S. M., Gann, P. H., Kopp, P., Colangelo, L., Longcope, C., & Liu, K. (2002). Serum Androgen Concentrations in Young Men: A Longitudinal

Analysis of Associations with Age, Obesity, and Race. *Cancer Epidemiology and Prevention Biomarkers*, *11(10)*, 1041-1047.

Geldart, S., Maurer, D., & Carney, K. (1999). Effects of eye size on adults' aesthetic ratings of faces and 5-month-olds' looking times. *Perception*, *28*(3), 361-374. doi: 10.1068/p2885

Ginsburg, E., Livshits, G., Yakovenko, K., & Kobyliansky, E. (1999). Genetics of human body size and shape: Evidence for an oligogenic control of adiposity. *Annals of Human Biology, 26,* 79-87. doi: 10.1080/030144699282994

Girard, M. P., Reed, Z. H., Friede, M., & Kieny, M. P. (2007). A review of human vaccine research and development: Malaria. *Vaccine, 25*, 1567-1580. doi:
10.1016/j.vaccine.2006.09.074

Glass, R. I., Parashar, U. D., & Estes, M. K. (2009). Norovirus gastroenteritis. *The New England Journal of Medicine, 361*, 1776-1785. doi: 10.1056/NEJMra0804575

Gonzalez-Santoyo, I., Wheatley, J. R., Welling, L. L., Cárdenas, R. A., Jimenez-Trejo, F., Dawood, K., & Puts, D. A. (2015). The face of female dominance: Women with dominant faces have lower cortisol. *Hormones and behavior*, *71*, 16-21. doi: 10.1016/j.yhbeh.2015.03.006

Grabe, S., Ward, L., & Hyde, J. S. (2008). The role of the media in body image concerns among women: A meta-analysis of experimental and correlational studies. *Psychological Bulletin, 134(3)*, 460–476. doi: 10.1037/0033-2909.134.3.460

Grammer, K., & Thornhill, R. (1994). Human (Homo sapiens) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108(3)*, 233-242.

Gray, A. W., & Boothroyd, L. G. (2012). Female facial appearance and health. *Evolutionary Psychology, 10*, 66-77. doi: 10.1177/147470491201000108

Guh, D. P., Zhang, W., Bansback N, Amarsi, Z., Laird Birmingham, C., & Anis, A. H. (2009). The incidence of co-morbidities related to obesity and overweight: A systematic review and meta-analysis. *BMC Public Health, 9*, 88. doi: 10.1186/1471-2458-9-88

Hamermesh, D. S., & Biddle, J. E. (1994). Beauty and the labor market. *The American Economic Review, 84*, 1174–1194.

Han, C., Hahn, A. C., Fisher, C. I., Debruine, L. M., & Jones, B. C. (2016). Women's facial attractiveness is related to their body mass index but not their salivary cortisol. *American Journal of Human Biology, 28*, 352-355. doi: 10.1002/ajhb.22792

Han, T. S., Morrison, C. E., & Lean, M. E. (1999). Age and health indications assessed by silhouette photographs. *European Journal of clinical Nutrition, 53,* 606-611. doi: 10.1038/sj.ejcn.1600816

Han, C., Wang, H., Hahn, A., Fisher, C., Kandrik, M., Fasolt, V., . . . Jones, B. (In prep). Cross-cultural differences in facial attractiveness judgments: Evidence from White UK and Chinese participants' preferences for experimentally manipulated facial coloration.

Hancock, P. J., & DeBruine, L. M. (2003). What's a face worth: Noneconomic factors in game playing. *Behavioral and Brain Sciences*, *26*(02), 162-163.

Hanna, J. L. (2010). Dance and sexuality: many moves. *Journal of sex research*, *47(2-3)*, 212-241. doi: 10.1080/00224491003599744

Havlicek, J., & Roberts, C. (2009). MHC-correlated mate choice in humans: A review. *Psychoneuroendocrinology, 34,* 497-512. doi: 10.1016/j.psyneuen.2008.10.007

Hebebrand, J., Wulftange, H., Goerg, T., Ziegler, A., Hinney, A., Barth, N., . . . Remschmidt, H. (2000). Epidemic obesity: Are genetic factors involved via increased rates of assortative mating? *International Journal of Obesity and Related Metabolic Disorders, 24,* 345-353. doi: 10.1038/sj.ijo.0801135

Henderson, J. J., & Anglin, J. M. (2003). Facial attractiveness predicts longevity. *Evolution and Human Behavior*, *24(5)*, 351-356. doi: 10.1016/S1090-5138(03)00036-9

Henderson, A. J., Holzleitner, I. J., Talamas, S. N., & Perrett, D. I. (2016). Perception of health from facial cues. *Philosophical Transactions of the Royal Society: Biological Sciences*, *371*, 20150380.

Holland, G., & Tiggemann, M. (2016). A systematic review of the impact of the use of social networking sites on body image and disordered eating outcomes. *Body image*, *17*, 100-110. doi: 10.1016/j.bodyim.2016.02.008

Holmes, S. J., & Hatch, C. E. (1938). Personal appearance as related to scholastic records and marriage selection in college women. *Human Biology*, *10(1)*, 65-76.

Hong, G., Luo, M. R., & Rhodes, P. A. (2001). A study of digital camera colorimetric characterisation based on polynomial modelling. *Color Research and Application, 26,* 76-84.

Hosoda, M., Stone-Romero, E. F., & Coats, G. (2003). The effects of physical attractiveness on job-related outcomes: A meta-analysis of experimental studies. *Personnel Psychology*, *56(2)*, 431-462. doi: 10.1111/j.1744-6570.2003.tb00157.x

Hughes, S. M., Dispenza, F., & Gallup, G. G. (2004). Ratings of voice attractiveness predict sexual behavior and body configuration. *Evolution and Human Behavior*, *25*, 295-304. doi: 10.1016/j.evolhumbehav.2004.06.001

Hughes, S. M., & Gallup, G. G. (2003). Sex differences in morphological predictors of sexual behavior: Shoulder to hip and waist to hip ratios. *Evolution and Human Behavior*, *24*, 173-178. doi: 10.1016/S1090-5138(02)00149-6

Hugill N., Fink B., Neave N. and Seydel H. (2009). Men's physical strength is associated with women's perceptions of their dancing ability. *Personality and Individual Differences, 47*, 527–530. doi: 10.1016/j.paid.2009.04.009

Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of “quality” in women and men. *Evolution and Human Behavior*, *22(2)*, 93-112.

Jacobson, P., Torgerson, J. S., Sjostrom, L., & Bouchard, C. (2007). Spouse resemblance in body mass index: Effects on adult obesity prevalence in the offspring generation. *American Journal of Epidemiology, 165,* 101-108. doi:10.1093/aje/kwj342

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings: Biological Sciences, 271*, 1213–1217. doi: 10.1098/rspb.2004.2712

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone-mediated adaptive design. *Evolution and Human Behavior*, *22(4)*, 251-267.

Jones, B. C., DeBruine, L. M., & Little, A. C. (2007a). The role of symmetry in attraction to average faces. *Perception & Psychophysics*, *69(8)*, 1273-1277.

Jones, B. C., DeBruine, L. M., Little, A. C., & Feinberg, D. R. (2007b). The valence of experience with faces influences generalized preferences. *Journal of Evolutionary Psychology, 5,* 119–129. doi: 10.1556/JCEP.5.2007.1–4.1

Jones, B. C., Feinberg, D. R., Watkins, C. D., Fincher, C. L., Little, A. C., & DeBruine, L. M. (2013a). Pathogen disgust predicts women's preferences for masculinity in men's voices, faces, and bodies. *Behavioral Ecology*, *24(2)*, 373-379. doi: 10.1093/beheco/ars173

Jones, B. C., Fincher, C. L., Welling, L. L. M., Little, A. C., Feinberg, D. R., Watkins, C. D., Al-Dujaili, E. A. S., & DeBruine, L. M. (2013b). Salivary cortisol and pathogen disgust predict men's preferences for feminine shape cues in women's faces. *Biological Psychology*, *92*, 233-240. doi: 10.1016/j.biopsycho.2012.11.014

Jones, B. C., Hahn, A. C., Fisher, C. I., Wincenciak, J., Kandrik, M., Roberts, S. C., Little, A.C., & DeBruine, L. M. (2015). Facial coloration tracks changes in women's estradiol. *Psychoneuroendocrinology*, *56*, 29-34. doi: 10.1016/j.psyneuen.2015.02.021

Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations.

Human Nature, *4(3)*, 271-296. doi: 10.1007/BF02692202

Jones, B. C., Little, A. C., Feinberg, D. R., Penton-Voak, I. S., Tiddeman, B. P., & Perrett, D. I. (2004). The relationship between shape symmetry and perceived skin condition in male facial attractiveness. *Evolution and Human Behavior*, *25(1)*, 24-30. doi: 10.1016/S1090-5138(03)00080-1

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgements of apparent health: Support for a "good genes" explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior*, *22(6)*, 417-429.

Jones, A. L., Porcheron, A., Sweda, J. R., Morizot, F., & Russel, R. (2016). Coloration in different areas of facial skin is a cue to health: The role of cheek redness and periorbital luminance in health perception. *Body Image, 17*, 57–66. doi: 10.1016/j.bodyim.2016.02.001

Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., . . . Burt, D. M. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London B: Biological Sciences*, *272(1561)*, 347-354. doi: 10.1098/rspb.2004.2962

Kahan, S. M., Liu, G., Reinhard, M. K., Hsu, C. C., Livingston, R. S., & Karst, S. M. (2011). Comparative murine norovirus studies reveal a lack of correlation between intestinal virus titers and enteric pathology. *Virology, 421(2)*, 202-210. doi: 10.1016/j.virol.2011.09.030

Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological science*, *9(1)*, 8-13.

Khaw, K. T., & Barrett-Connor, E. (1992). Lower endogenous androgens predict central adiposity in men. *Annals of Epidemiology, 2(5)*, 675–682. doi: 10.1016/1047-2797(92)90012-F

Kissler, J., & Bäuml, K. H. (2000). Effects of the beholder's age on the perception of facial attractiveness. *Acta Psychologica, 104(2)*, 145–166. doi: 10.1016/S0001-6918(00)00018-4

Kniffin, K. M., & Wilson, D. S. (2004). The effect of nonphysical traits on the perception of physical attractiveness: Three naturalistic studies. *Evolution and Human Behavior*, *25(2)*, 88-101. doi: 10.1016/j.evolhumbehav.2004.01.002

Kowner, R. (1996). Facial asymmetry and attractiveness judgement in developmental perspective. *Journal of Experimental Psychology: Human Perception and Performance*, *22(3)*, 662. doi: 10.1037/0096-1523.22.3.662

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological bulletin*, *126(3)*, 390-423. doi: 10.1037//0033-2909.126.3.390

Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science*, *1(2)*, 115-121.

Langlois, J. H., Roggman, L. A., & Musselman, L. (1994). What is average and what is not average about attractive faces? *Psychological Science*, *5(4)*, 214-220. doi: 10.1111/j.1467-9280.1994.tb00503.x

Lee, A. J., Dubbs, S. L., Kelly, A. J., von Hippel, W., Brooks, R. C., & Zietsch, B. P. (2013). Human facial attributes, but not perceived intelligence, are used as cues of health and resource provision potential. *Behavioral Ecology, 24*, 779-787. doi: 10.1093/beheco/ars199

Lefevre, C. E., Ewbank, M. P., Calder, A. J., von dem Hagen, E., & Perrett, D. I. (2013). It is all in the face: Carotenoid skin coloration loses attractiveness outside the face. *Biology Letters, 9,* 20130633. doi: 10.1098/rsbl.2013.0633

Lefevre, C. E., & Perrett, D. I. (2014). Fruit over sunbed: Carotenoid skin colouration is found more attractive than melanin colouration. *The Quarterly Journal of Experimental Psychology, 68*, 284–293. doi: 10.1080/17470218.2014.944194

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution*, *62(10)*, 2473-2486. doi: 10.1111/j.1558-5646.2008.00478.x

Lieberman, D. L., Tybur, J. M., & Latner, J. D. (2011). Disgust sensitivity, obesity stigma, and gender: Contamination psychology predicts weight bias for women, not men. *Obesity, 20*, 1803-1814. doi: 10.1038/oby.2011.247

Little, A. C., Apicella, C. L., & Marlowe, F. W. (2007). Preferences for symmetry in human faces in two cultures: Data from the UK and the Hadza, an isolated group of hunter-gatherers. *Proceedings of the Royal Society of London B: Biological Sciences*, *274(1629)*, 3113-3117. doi: 10.1098/rspb.2007.0895

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011c). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society of London B, 278*, 2032-2039. doi: 10.1098/rspb.2010.1925

Little, A. C., & Hancock, P. J. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *British Journal of Psychology*, *93(4)*, 451-464. doi: 10.1348/000712602761381349

Little, A. C., & Jones, B. C. (2003). Evidence against perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London B: Biological Sciences*, *270(1526)*, 1759-1763. doi: 10.1098/rspb.2003.2445

Little, A. C., & Jones, B. C. (2006). Attraction independent of detection suggests special mechanisms for symmetry preferences in human face perception. *Proceedings of the Royal Society of London B: Biological Sciences*, *273(1605)*, 3093-3099. doi: 10.1098/rspb.2006.3679

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011b). Facial attractiveness: Evolutionary based research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1571), 1638-1659. doi: 10.1098/rstb.2010.0404

Little, A. C., Jones, B. C., DeBruine, L. M., & Caldwell, C. A. (2011a). Social learning and human mate preferences: A potential mechanism for generating and maintaining between-population diversity in attraction. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366(1563)*, 366-375. doi: 10.1098/rstb.2010.0192

Little, A. C., Jones, B. C., Feinberg, D. R., & Perrett, D. I. (2014). Men's strategic preferences for femininity in female faces. *British Journal of Psychology*, *105*, 364-381. doi: 10.1111/bjop.12043

Little, A. C., & Mannion, H. (2006). Viewing attractive or unattractive same-sex individuals changes self-rated attractiveness and face preferences in women. *Animal Behaviour, 72,* 981–987. doi: 10.1016/j.anbehav.2006.01.026

Main, J. C., DeBruine, L. M., Little, A. C., & Jones, B. C. (2010). Interactions among the effects of head orientation, emotional expression, and physical attractiveness on face preferences. *Perception*, *39(1)*, 62-71. doi: 10.1068/p6503

Marlowe, C. M., Schneider, S. L., & Nelson, C. E. (1996). Gender and attractiveness biases in hiring decisions: Are more experienced managers less biased? *Journal of applied psychology*, *81(1)*, 11-21.

Matts, P. J., Fink, B., Grammer, K., & Burquest, M. (2007). Color homogeneity and visual perception of age, health, and attractiveness of female facial skin. *Journal of the American Academy of Dermatology*, *57(6)*, 977-984. doi: 10.1016/j.jaad.2007.07.040

McArthur, L. Z., & Berry, D. S. (1987). Cross-cultural agreement in perceptions of babyfaced adults. *Journal of Cross-Cultural Psychology*, *18(2)*, 165-192.

McCarty, K., Hönekopp, J., Neave, N., Caplan, N., & Fink, B. (2013). Male body movements as possible cues to physical strength: A biomechanical analysis. *American Journal of Human Biology*, *25(3)*, 307-312. doi: 10.1002/jhb.22360

Mealey, L., Bridgstock, R., & Townsend, G. C. (1999). Symmetry and perceived facial attractiveness: A monozygotic co-twin comparison. *Journal of Personality and Social Psychology*, *76(1)*, 151-158. doi: 10.1037/0022-3514.76.1.151

Mitton, J. B., & Grant, M. C. (1984). Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annual Review of Ecology and Systematics*, *15*, 479-499. doi: 10.1146/annurev.es.15.110184.002403

Mobius, M. M., & Rosenblat, T. S. (2006). Why beauty matters. *The American Economic Review*, *96(1)*, 222-235.

Møller, A. P. (1994). *Sexual selection and the barn swallow.* New York: Oxford University Press.

Møller, A. P. (1997). Developmental stability and fitness: A review. *The American Naturalist*, *149(5)*, 916-932. doi: 10.1086/286030

Möller, R., Tafeit, E., Pieber, T. R., Sudi, K., & Reibnegger, G. (2000). Measurement of subcutaneous adipose tissue topography (SAT-Top) by means of a new optical device, LIPOMETER, and the evaluation of standard factor coefficients in healthy subjects. *American Journal of Human Biology*, *12(2)*, 231-239. doi: 10.1002/(SICI)1520-6300(200003/04)12:2<231::AID-AJHB9>3.0.CO;2-X

Moore, F. R., Al Dujaili, E. A. S., Cornwell, R. E., Law Smith, M. J., Lawson, J. F., Sharp, M., & Perrett, D. I. (2011a). Cues to sex- and stress-hormones in the human male face: Functions of glucocorticoids in the immunocompetence handicap hypothesis. *Hormones and Behavior, 60*, 269–274. doi: 10.1016/j.yhbeh.2011.05.010

Moore, F. R., Coetzee, V., Contreras-Garduno, J., Debruine, L. M., Kleisner, K., Krams, I., . . . Suzuki, T. N. (2013). Cross-cultural variation in women's preferences for cues to sex- and stress-hormones in the male face. *Biology Letters, 9*, 20130050. doi: 10.1098/rsbl.2013.0050

Moore, F. R., Cornwell, R. E., Law Smith, M. J., Al Dujaili, E. A. S., Sharp, M., &

Perrett, D. I. (2011b). Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. *Proceedings of the Royal Society of London B, 278,* 774–780. doi: 10.1098/rspb.2010.1678

Moore, M. E., Stunkard, A., & Srole, L. (1997). Obesity, social class, and mental illness. *Obesity Research, 5,* 503-508. doi: 10.1002/j.1550-8528.1997.tb00678.x

Mungall, A. J., Palmer, S. A., Sims, S. K., Edwards, C. A., Ashurst, J. L., Wilming, L., . . . Beck, S. (2003). The DNA sequence and analysis of human chromosome 6. *Nature, 425*, 805–811. doi: 10.1038/nature02055

Neave, N., McCarty, K., Freynik, J., Caplan, N., Hönekopp, J., & Fink, B. (2010). Male dance moves that catch a woman's eye. *Biology Letters*, rsbl20100619. doi: 10.1098/rsbl.2010.0619

Nedelec, J. L., & Beaver, K. M. (2014). Physical attractiveness as a phenotypic marker of health: An assessment using a nationally representative sample of American adults. *Evolution and Human Behavior*, *35(6)*, 456-463. doi: 10.1016/j.evolhumbehav.2014.06.004

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41(2)*, 147-155.

Park, J. H., Schaller, M., & Crandall, C. S. (2007). Pathogen-avoidance mechanisms and the stigmatization of obese people. *Evolution and Human Behavior, 28*, 410–414. doi: 10.1016/j.evolhumbehav.2007.05.008

Pasco, J. A., Nicholson, G. C., Brennan, S. L., & Kotowicz, M. A. (2012). Prevalence of obesity and the relationship between the body mass index and body fat: Cross-sectional population-based data. *PLoS One, 7*, e29580. doi: 10.1371/journal.pone.0029580

Pasquali, R., Casimirri, F., Cantobelli, S., Melchionda, N., Morselli Labate, A. M., Fabbri, R., . . . Bortoluzzi, L. (1991). Effect of obesity and body fat distribution on sex hormones and insulin in men. *Metabolism, 40(1)*, 101-104. doi: 10.1016/0026-0495(91)90199-7

Penke, L., & Asendorpf, J. B. (2008). Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of Personality and Social Psychology*, *95*, 1113-1135. doi: 10.1037/0022-3514.95.5.1113

Penton-Voak, I. S. (2011). In retreat from nature? Successes and concerns in Darwinian approaches to facial attractiveness. *Journal of Evolutionary Psychology, 1,* 1–21. doi: 10.1556/JEP.9.2011.2.5

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., & Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London B: Biological Sciences*, *268(1476)*, 1617-1623. doi: 10.1098/rspb.2001.1703

Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (Homo sapiens). *Journal of Comparative Psychology*, *117*, 264-271. doi: 10.1037/0735-7036.117.3.264

Perilloux, C., Cloud, J. M., & Buss, D. M. (2013). Women's physical attractiveness and short-term mating strategies. *Personality and Individual Differences*, *54*, 490-495. doi: 10.1016/j.paid.2012.10.028

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, *20(5)*, 295-307. doi: 10.1016/S1090-5138(99)00014-8

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., … Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394(6696)*, 884-887. doi: 10.1038/29772

Perrett, D., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., Schmidt, N., … Barrett, L. (2002). Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London B, 269,* 873-880. doi: 10.1098/rspb.2002.1971

Peters, M., Rhodes, G., & Simmons, L. W. (2007). Contributions of the face and body to overall attractiveness. *Animal Behaviour, 73,* 937–942. doi: 10.1016/j.anbehav.2006.07.012

Pisanski, K., Fraccaro, P. J., Tigue, C. C., O'Connor, J. J. M., Röder, S., Andrews, P. … Feinberg, D. R. (2014). Vocal indicators of body size in men and women: A meta-analysis. *Animal Behaviour, 95*, 89-99. doi: 10.1016/j.anbehav.2014.06.011

Pisanski, K., Jones, B. C., Fink, B., O'Connor, J. J. M., Debruine, L. M., Roder, S., & Feinberg, D. R. (2015). Voice parameters predict sex-specific body morphology in men and women. *Animal Behaviour, 112*, 13-22. doi: 10.1016/j.anbehav.2015.11.008

Pound, N., Lawson, D. W., Toma, A. M., Richmond, S., Zhurov, A. I., & Penton-Voak, I. S. (2014). Facial fluctuating asymmetry is not associated with childhood ill-health in a large British cohort study. *Proceedings of the Royal*

Society of London B: Biological Sciences, *281(1792)*, 20141639. doi: 10.1098/rspb.2014.1639

Price, M. E., Pound, N., Dunn, J., Hopkins, S., & Kang, J. (2013). Body shape preferences: Associations with rater body shape and sociosexuality. *PLoS One, 8*, e52532. doi: 10.1371/journal.pone.0052532

Puts, D. A., Jones, B. C., & DeBruine, L. M. (2012). Sexual selection on human faces and voices. *Annual Review of Sex Research, 49,* 227-243. doi: 10.1080/00224499.2012.658924

Ramlau-Hansen, C. H., Thulstrup, A. M., Nohr, E. A., Bonde, J. P., Sørensen, T. I. A., & Olsen, J. (2007). Subfecundity in overweight and obese couples. *Human Reproduction, 22,* 1634-1637. doi: 10.1093/humrep/dem035

Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., … Krams, I. (2013a). Adiposity, compared to masculinity, serves as a more valid cue to immunocompetence in human mate choice. *Proceedings of the Royal Society of London B, 280*, 20122495. doi: 10.1098/rspb.2012.2495

Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., … Krams, I. (2013b). Facial attractiveness is related to women’s cortisol and body fat, but not with immune responsiveness. *Biology Letters, 9*, 20130255. doi: 10.1098/rsbl.2013.0255

Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., & Krams, I. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications*, *3*, 694. doi: 10.1038/ncomms1696

Re, D. E., Coetzee, V., Xiao, D., Buls, D., Tiddeman, B. P., Boothroyd, L. G., & Perrett, D. I. (2011b). Viewing heavy bodies enhances preferences for facial adiposity. *Journal of Evolutionary Psychology*, *9(4)*, 295-308. doi: 10.1556/JEP.9.2011.4.2

Re, D. E., & Perrett, D. I. (2014). The effects of facial adiposity on attractiveness and perceived leadership ability. *The Quarterly Journal of Experimental Psychology*, *67(4)*, 676-686. doi: 10.1080/17470218.2013.825635

Re, D. E., Whitehead, R. D., Xiao, D., & Perrett, D. I. (2011a). Oxygenated-blood colour change thresholds for perceived facial redness, health, and attractiveness. *PloS one*, *6(3)*, e17859. doi: 10.1371/journal.pone.0017859

Reither, E. N., Hauser, R. M., & Swallen, K. C. (2009). Predicting adult health and mortality from adolescent facial characteristics in yearbook photographs. *Demography, 46*, 27–41. doi: 10.1353/dem.0.0037

Rennels, J. L., Bronstad, P. M., & Langlois, J. H. (2008). Are attractive men's faces masculine or feminine? The importance of type of facial stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *34(4)*, 884-893. doi: 10.1037/0096-1523.34.4.884

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology, 57,* 199-226. doi: 10.1146/annurev.psych.57.102904.190208

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003a). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, S93-S95. doi: 10.1098/rsbl.2003.0023

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: Are supermale and superfemale faces super-attractive? *British Journal of Psychology*, *91(1)*, 125-140. doi: 10.1348/000712600161718

Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W. G., & Nakayama, K. (2003b). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science, 14(6)*, 558–566. doi: 10.1046/j.0956-7976.2003.psci_1465.x

Rhodes, G., Proffitt, F., Grady, J. M., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin & Review*, *5(4)*, 659-669. doi: 10.3758/BF03208842

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: Does attractiveness enhance mating success? *Evolution and Human Behavior*, *26*, 186-201. doi: 10.1016/j.evolhumbehav.2004.08.014

Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R., & Akamatsu, S. (2001). Attractiveness of facial averageness and symmetry in non-Western cultures: In search of biologically based standards of beauty. *Perception*, *30(5)*, 611-625. doi: 10.1068/p3123

Rhodes, G., Yoshikawa, S., Palermo, R., Simmons, L. W., Peters, M., Lee, K., ... & Crawford, J. R. (2007). Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. *Perception*, *36(8)*, 1244-1252. doi: 10.1068/p5712

Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Carter, V., Jones, B. C., … Petrie, M. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, *26(3)*, 213-226. doi: 10.1016/j.evolhumbehav.2004.09.002

Rosenberg, S. W., Bohan, L., McCafferty, P., & Harris, K. (1986). The image and the vote: The effect of candidate presentation on voter preference. *American Journal of Political Science*, 108-127. doi: 10.2307/2111296

Rosenblum, G. D., & Lewis, M. (1999). The relations among body image, physical attractiveness, and body mass in adolescence. *Child Development*, *70(1)*, 50-64.

Rubenstein, A. J., Kalakanis, L., & Langlois, J. H. (1999). Infant preferences for attractive faces: A cognitive explanation. *Developmental Psychology*, *35(3)*, 848-855. doi: 10.1037/0012-1649.35.3.848

Samuels, C. A., Butterworth, G., Roberts, T., Graupner, L., & Hole, G. (1994). Facial aesthetics: Babies prefer attractiveness to symmetry. *Perception, 23*, 823–831.

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews, 21*, 55-89. doi: 10.1210/edrv.21.1.0389

Saxton, T. K., Caryl, P. G., & Craig Roberts, S. (2006). Vocal and facial attractiveness judgments of children, adolescents and adults: the ontogeny of mate choice. *Ethology*, *112(12)*, 1179-1185. doi: 10.1111/j.1439-0310.2006.01278.x

Saxton, T. K., DeBruine, L. M., Jones, B. C., Little, A. C., & Roberts, S. C. (2009). Face and voice attractiveness judgments change during adolescence. *Evolution and Human Behavior, 30(6)*, 398–408. doi: 10.1016/j.evolhumbehav.2009.06.004

Saxton, T. K., DeBruine, L. M., Jones, B. C., Little, A. C., & Roberts, S. C. (2011). A longitudinal study of adolescents' judgments of the attractiveness of facial symmetry, averageness and sexual dimorphism. *Journal of Evolutionary Psychology, 9(1),* 43–55. doi: 10.1556/JEP.9.2011.22.1

Schaller, M. (2006). Parasites, behavioral defenses, and the social psychological mechanisms through which cultures are evoked. *Psychological Inquiry, 17*, 96-101. doi: 10.1207/s15327965pli1702_2

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London B: Biological Sciences*, *266(1431)*, 1913-1917. doi: 10.1098/rspb.1999.0866

Scherf, K. S., Behrmann, M., & Dahl, R. E. (2012). Facing changes and changing faces in adolescence: A new model for investigating adolescent-specific interactions between pubertal, brain and behavioral development. *Developmental Cognitive Neuroscience*, *2(2)*, 199-219. doi: 10.1016/j.dcn.2011.07.016

Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences*, *28*, 247-275.

Schneider, T. M., Hecht, H., & Carbon, C-C. (2012). Judging body weight from faces: The height-weight illusion. *Perception, 41*, 12-124. doi: 10.1068/p7140

Schwartz, C. R., & Mare, R. D. (2005). Trends in educational assortative marriage from 1940 to 2003. *Demography, 42,* 621-46. doi: 10.1353/dem.2005.0036

Scott, I. M., Clark, A. P., Boothroyd, L. G., & Penton-Voak, I. S. (2012). Do men’s faces really signal heritable immunocompetence? *Behavioral Ecology, 24*, 579–589. doi: 10.1093/beheco/ars092

Scott, I. M., Clark, A. P., Josephson, S. C., Boyette, A. H., Cuthill, I. C., Fried, R.

L., … Honey, P. L. (2014). Human preferences for sexually dimorphic faces may be evolutionarily novel. *Proceedings of the National Academy of Sciences*, *111(40)*, 14388-14393. doi: 10.1073/pnas.1409643111

Scott, I., Swami, V., Josephson, S. C., & Penton-Voak, I. S. (2008). Context-dependent preferences for facial dimorphism in a rural Malaysian population. *Evolution and Human Behavior*, *29(4)*, 289-296. doi: 10.1016/j.evolhumbehav.2008.02.004

Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society of London B: Biological Sciences*, *276(1656)*, 575-584. doi: 10.1098/rspb.2008.1177

Setchell, J. M., Wickings, E. J., & Knapp, L. A. (2006). Signal content of red facial coloration in female mandrills (Mandrillus sphinx). *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 2395-2400. doi: 10.1098/rspb.2006.3573

Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and physical health. *Evolution and human behavior, 20*, 71–76.

Shelton, K. E., Woodson, H., Gay, S., & Suratt, P. M. (1993). Pharyngeal fat in obstructive sleep apnea. *The American Review of Respiratory Disease, 148*, 462-466. doi: 10.1164/ajrccm/148.2.462

Shinada, M., & Yamagishi, T. (2014). Physical attractiveness and cooperation in a prisoner's dilemma game. *Evolution and Human Behavior*, *35(6)*, 451-455. doi: 10.1016/j.evolhumbehav.2014.06.003

Sies, H., Stahl, W., & Sevanian, A. (2005). Nutritional, dietary and postprandial oxidative stress. *The Journal of Nutrition*, *135(5)*, 969-972.

Silventoinen, K., Kaprio, J., Lahelma, E., Viken, R. J., & Rose, R. J. (2003). Assortative mating by body height and BMI: Finnish twins and their spouses. *American Journal of Human Biology, 15,* 620-627. doi: 10.1002/ajhb.10183

Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology*, *60*, 870-883. doi: 10.1037/0022-3514.60.6.870

Slater, A., Quinn, P. C., Hayes, R., & Brown, E. (2000). The role of facial orientation in newborn infants' preference for attractive faces. *Developmental Science*, *3(2)*, 181-185. doi: 10.1111/1467-7687.00111

Slater, A., Von der Schulenburg, C., Brown, E., Badenoch, M., Butterworth, G., Parsons, S., & Samuels, C. (1998). Newborn infants prefer attractive faces. *Infant Behavior and Development*, *21(2)*, 345-354. doi: 10.1016/S0163-6383(98)90011-X

Smith, F. G., Jones, B. C., DeBruine, L. M., & Little, A. C. (2009). Interactions between masculinity-femininity and apparent health in face preferences. *Behavioral Ecology, 20(2)*, 441-445. doi: 10.1093/beheco/arn141

Smith, C. V. & Shaffer, M. J. (2013). Gone but not forgotten: Virginity loss and current sexual satisfaction. *Journal of Sex & Marital Therapy, 39*, 96-111. doi: 10.1080/0092623X.2012.675023

Smits, J. (2003). Social closure among the higher educated: Trends in educational homogamy in 55 countries. *Social Science Research, 32,* 251-277. doi: 10.1016/S0049-089X(02)00049-2

Solnick, S. J., & Schweitzer, M. E. (1999). The influence of physical attractiveness and gender on ultimatum game decisions. *Organizational Behavior and Human Decision Processes*, *79(3)*, 199-215.

Speakman, J. R., Djafarian, K., Stewart, J., & Jackson, D. M. (2007). Assortative mating for obesity. *American Journal of Clinical Nutrition, 86,* 316-323.

Speliotes, E. K., Willer, C. J., Berndt, S. I., Monda, K. L., Thorleifsson, G., Jackson, A. U., …Loos, R. J. F. (2010). Association analyses of 249,796 individuals reveal eighteen new loci associated with body mass index. *Nature Genetics, 42,* 937-948. doi: 10.1038/ng.686

Spitzer, B. L., Henderson, K. A., & Zivian, M. T. (1999). Gender differences in population versus media body sizes: A comparison over four decades. *Sex Roles*, *40*, 545-565. doi: 10.1023/A:1018836029738

Stamatas, G. N., Zmudzka, B. Z., Kollias, N., & Beer, J. Z. (2004). Non-invasive measurements of skin pigmentation in situ. *Pigment Cell Research*, *17(6)*, 618-626. doi: 10.1111/j.1600-0749.2004.00204.x

Stephen, I. D., Coetzee, V., Law Smith, M., & Perrett, D. I. (2009b). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS One, 4*, e5083. doi: 10.1371/journal.pone.0005083

Stephen, I. D., Coetzee, V., & Perrett, D. I. (2011). Carotenoid and melanin pigment coloration affect perceived human health. *Evolution and Human Behavior, 32*, 216–227. doi: 10.1016/j.evolhumbehav.2010.09.003

Stephen, I. D., Law Smith, M. J., Stirrat, M. R., & Perrett, D. I. (2009a). Facial skin coloration affects perceived health of human faces. *International Journal of Primatology, 30*, 845–857.

Stephen, I. D., Oldham, F. H., Perrett, D. I., & Barton, R. A. (2012a). Redness enhances perceived aggression, dominance and attractiveness in men's faces. *Evolutionary Psychology, 10*, 562-572. doi:10.1007/s10764-009-9380-z

Stephen, I. D., & Perera, A. T. M. (2014). Judging the differences between women's attractiveness and health: Is there really a difference between judgments made by men and women? *Body image*, *11(2)*, 183-186. doi: 10.1016/j.bodyim.2013.11.007

Stephen, I. D., Scott, I. M. L., Coetzee, V., Pound, N., Perrett, D. I., & Penton-Voak, I. S. (2012b). Cross-cultural effects of color, but not morphological masculinity, on perceived attractiveness of men's faces. *Evolution and Human Behavior, 33*, 260-267.

Stice, E. (1994). Review of the evidence for a sociocultural model of bulimia nervosa and an exploration of the mechanisms of action. *Clinical Psychology Review, 14(7)*, 633–661. doi: 10.1016/0272-7358(94)90002-7

Stillman, T. F., & Maner, J. K. (2009). A sharp eye for her SOI: Perception and misperception of female sociosexuality at zero acquaintance. *Evolution and Human Behavior*, *30*, 124-130. doi: 10.1016/j.evolhumbehav.2008.09.005

Sutherland, C. A. M., Oldmeadow, J. A., Santos, I. M., Towler, J., Burt, D. M., & Young, A. W. (2013). Social inferences from faces: Ambient images generate a three-dimensional model. *Cognition, 127*, 105-118. doi: 10.1016/j.cognition.2012.12.001

Takahashi, C., Yamagishi, T., Tanida, S., Kiyonari, T., & Kanazawa, S. (2006). Attractiveness and cooperation in social exchange. *Evolutionary Psychology*, *4(1)*, 315-329. doi: 10.1177/147470490600400127

Tan, K. W., Graf, B. A., Mitra, S. R., & Stephen, I. D. (2015). Daily consumption of a fruit and vegetable smoothie alters facial skin color. *PloS One*, *10(7)*, e0133445. doi: 10.1371/journal.pone.0133445

Thompson, J. K., Heinberg, L., Altabe, M., & Tantleff-Dunn, S. (1999). *Exacting beauty: Theory, assessment, and treatment of body image disturbance.* Washington, DC: American Psychological Association.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty. *Human Nature*, *4(3)*, 237-269. doi: 10.1007/BF02692201

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J. K., & Franklin, M. (2003). Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology*, *14(5)*, 668-678. doi: 10.1093/beheco/arg043

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, *27(2)*, 131-144. doi: 10.1016/j.evolhumbehav.2005.06.001

Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior*, *20(2)*, 105-120. doi: 10.1016/S1090-5138(98)00044-0

Thornhill, T., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews, 72*, 497–548.

Thursz, M. R., Thomas, H. C., Greenwood, B. M., & Hill, A. V. (1997).

Heterozygote advantage for HLA class-II type in hepatitis B virus infection. *Nature Genetics*, *17(1)*, 11-12. doi: 10.1038/ng0997-11

Tiddeman, B., Burt, D. M., & Perrett, D. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications, 21(5)*, 42-50. doi: 10.1109/38.946630

Tigue, C. C., Pisanski, K., O'Connor, J. J. M., Fraccaro, P. J., & Feinberg, D. R. (2012). Men's judgments of women's facial attractiveness from two- and three-dimensional images are similar. *Journal of Vision, 12*, 3. doi: 10.1167/12.12.3

Tinlin, R. M., Watkins, C. D., Welling, L. L. M., DeBruine, L. M., Al-Dujaili, E. A. S., & Jones, B. C. (2013). Perceived facial adiposity conveys information about women’s health. *British Journal of Psychology, 104*, 235–248. doi: 10.1111/j.2044-8295.2012.02117.x

Tovée, M. J., Emery, J. L., & Cohen−Tovée, E. M. (2000). The estimation of body mass and physical attractiveness is dependent on the observer’s own body mass index. *Proceedings of the Royal Society of London B, 267,* 1987–1997. doi: 10.1098/rspb.2000.1240

Tovée, M. J., Mason, S. M., Emery, J. L., McCluskey, S. E., & Cohen-Tovée, E. M. (1997). Supermodels: Stick insects or hourglasses? *The Lancet*, *350*, 1474-1475. doi: 10.1016/S0140-6736(05)64238-9

Tovee, M. J., Maisey, D. S., Emery, J. L., & Cornelissen, P. L. (1999). Visual cues to female physical attractiveness. *Proceedings of the Royal Society B, 266*, 211-218. doi: 10.1098/rspb.1999.0624

Tovee, M. J., Reinhardt, S., Emery, J. L., & Cornelissen, P. L. (1998). Optimum body-mass index and maximum sexual attractiveness. *Lancet, 352*, 548-548.

Tybur, J. M., Bryan, A. D., Lieberman, D., Caldwell Hooper, A. E., & Merriman, L. A. (2011). Sex differences and sex similarities in disgust sensitivity. *Personality and Individual Differences, 51(3),* 343-348. doi: 10.1016/j.paid.2011.04.003

Visser, M., Langlois, J., Guralnik, J. M., Cauley, J., Kronmal, R., Robbins, J., et al. (1998). High body fatness, but not low fat-free mass, predicts disability in older men and women: The Cardiovascular Health Study. *The American Journal of Clinical Nutrition, 68*, 584–590.

Vukovic, J., Feinberg, D., DeBruine, L., Smith, F., & Jones, B. (2010). Women's voice pitch is negatively correlated with health risk factors. *Journal of Evolutionary Psychology*, *8(3)*, 217–225. doi: 10.1556/JEP.8.2010.3.2

Waitt, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M., & Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, S144-S146. doi: 10.1098/rsbl.2003.0065

Wang, Y. (2001). Cross-national comparison of childhood obesity: The epidemic and the relationship between obesity and socioeconomic status. *International Journal of Epidemiology*, *30*, 1129-1136. doi: 10.1093/ije/30.5.1129

Wang, G., Djafarian, K., Egedigwe, C. A., El Hamdouchi, A., Ojiambo, R., Ramuth, H., … Speakman, J. R. (2015). The relationship of female physical attractiveness to body fatness. *PeerJ, 3*, e1155. doi: 10.7717/peerj.1155

Want, S. C. (2009). Meta-analytic moderators of experimental exposure to media portrayals of women on female appearance satisfaction: Social comparisons as automatic processes. *Body Image, 6*, 257–269. doi: 10.1016/j.bodyim.2009.07.008

Watson, D., Klohnen, E. C., Casillas, A., Simms, E. N., Haig, J., & Berry, D. S. (2004). Match makers and deal breakers: Analyses of assortative mating in newlywed couples. *Journal of Personality, 72(5),* 1029–68. doi: 10.1111/j.0022-3506.2004.00289.x

Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: a review. *Psychological Bulletin*, *131*, 635-653. doi: 10.1037/0033-2909.131.5.635

Weeden, J., & Sabini, J. (2007). Subjective and objective measures of attractiveness and their relation to sexual behavior and sexual attitudes in university students. *Archives of Sexual Behavior*, *36*, 79-88. doi: 10.1007/s10508-006-9075-x

Weege, B., Pham, M. N., Shackelford, T. K., & Fink, B. (2015). Physical strength and dance attractiveness: Further evidence for an association in men, but not in women. *American Journal of Human Biology*, *27(5)*, 728-730. doi: 10.1002/ajhb.22703

Wellens, R. I., Roche, A. F., Khamis, H. J., Jackson, A. S., Pollock, M. L., & Siervogel, R. M. (1996). Relationships between the body mass index and body composition. *Obesity research*, *4(1)*, 35-44. doi: 10.1002/j.1550-8528.1996.tb00510.x

Welling, L. L., Jones, B. C., DeBruine, L. M., Smith, F. G., Feinberg, D. R., Little, A. C., & Al-Dujaili, E. A. (2008). Men report stronger attraction to femininity in women's faces when their testosterone levels are high. *Hormones and Behavior*, *54(5)*, 703-708. doi: 10.1016/j.yhbeh.2008.07.012

Wiederman, M. W., & Hurst, S. R. (1998). Body size, physical attractiveness, and body image among young adult women: Relationships to sexual experience and sexual esteem. *Journal of Sex Research*, *35*, 272-281. doi: 10.1080/00224499809551943

Wilson, R. K., & Eckel, C. C. (2006). Judging a book by its cover: Beauty and expectations in the trust game. *Political Research Quarterly*, *59(2)*, 189-202. doi: 10.1177/106591290605900202

White, A. E., Kenrick, D. T., & Neuberg, S. L. (2013). Beauty at the ballot box: Disease threats predict preferences for physically attractive leaders. *Psychological Science*, *24(12)*, 2429-2436. doi: 10.1177/0956797613493642

Whitehead, R. D., Coetzee, V., Ozakinci, G., & Perrett, D. I. (2012b). Cross-cultural effects of fruit and vegetable consumption on skin colour. *American Journal of Public Health, 102(2)*, 212–213. doi: 10.2105/AJPH.2011.300495

Whitehead, R. D., Ozakinci, G., & Perrett, D. I. (2012c). Attractive skin coloration: Harnessing sexual selection to improve diet and health. *Evolutionary Psychology, 10*, 842–854. doi: 10.1177/147470491201000507

Whitehead, R. D., Perrett, D. I., & Ozakinci, G. (2011). Appealing to vanity: Does seeing the potential appearance-benefits of fruit and vegetable consumption motivate dietary change? *Annals of Behavioral Medicine*, *41(1)*, s214. doi: 10.2105/AJPH.2011.300405

Whitehead, R. D., Re, D., Xiao, D., Ozakinci, G., & Perrett, D. I. (2012a). You are what you eat: Within-subject increases in fruit and vegetable consumption confer beneficial skin-color changes. *PLoS One, 7*, e32988. doi: 10.1371/journal.pone.0032988

Winkler, C., & Rhodes, G. (2005). Perceptual adaptation affects attractiveness of female bodies. *British Journal of Psychology, 96*, 141–154. doi: 10.1348/000712605X36343

World Health Organization (2000). *Obesity: Preventing and managing the global epidemic.* Geneva: World Health Organization.

Yanover, T., & Thompson, J. K. (2010). Perceptions of health and attractiveness: The effects of body fat, muscularity, gender, and ethnicity. *Journal of Health Psychology, 15*, 1039-1048. doi: 10.1177/1359105309360426

Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to “bad genes” and the anomalous face overgeneralization effect: Cue validity, cue utilization, and accuracy in judging intelligence and health. *Journal of Nonverbal Behavior*, *28(3)*, 167-185. doi: 10.1023/B:JONB.0000039648.30935.1b

Zietsch, B. P., Verweij, K. J. H., Heath, A. C., & Martin, N. G. (2011). Variation in human mate choice: Simultaneously investigating heritability, parental influence, sexual imprinting, and assortative mating. *The American Naturalist, 177,* 605-616. doi: 10.1086/659629

Zuk, M. (1992). The role of parasites in sexual selection: Current evidence and future directions. *Advances in the Study of Behavior*, *21*, 39-68.