



Han, Chengyang (2018) *Facial appearance as a cue of physical condition*. PhD thesis.

<https://theses.gla.ac.uk/8788/>

Copyright and moral rights for this work are retained by the author

A copy can be downloaded for personal non-commercial research or study, without prior permission or charge

This work cannot be reproduced or quoted extensively from without first obtaining permission in writing from the author

The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the author

When referring to this work, full bibliographic details including the author, title, awarding institution and date of the thesis must be given

Enlighten: Theses

<https://theses.gla.ac.uk/>
research-enlighten@glasgow.ac.uk

Facial Appearance As A Cue of Physical Condition

Chengyang Han

M.Sc.

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

Institute of Neuroscience & Psychology

College of Science and Engineering

University of Glasgow

November 2017

Publication statement

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

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(3), 352-355.

Han, C., Kandrik, M., Hahn, A. C., Fisher, C. I., Feinberg, D. R., Holzleitner, I. J., DeBruine, L. M., & Jones, B. C. (2017). Interrelationships among men's threat potential, facial dominance, and vocal dominance. *Evolutionary Psychology*, 15(1), 1474704917697332.

Han, C., Wang, H., Hahn, A. C., Fisher, C. I., Kandrik, M., Fasolt, V., Morrison, D. K., Lee, A. L., Holzleitner, A. J., DeBruine, L. M., & Jones, B. C. (In Press). Cultural differences in preferences for facial coloration. *Evolution and Human Behavior*.

Abstract

Social judgments of facial appearance may reflect that individual's physical condition. In this thesis, I present empirical studies investigating social judgments of facial appearance and their underlying physiology. The first empirical chapter investigates the relationship between social judgments of women's facial appearance and their salivary cortisol levels and body mass index (BMI). Faces of women with lower BMI were rated as more attractive, healthier, and more feminine. By contrast with previous research, social judgments of women's faces were not related to their salivary cortisol, however. These results suggest that the type of health information reflected in women's faces includes qualities indexed by BMI, but does not necessarily include qualities indexed by cortisol.

In my second empirical chapter, I investigated the interrelationships among a composite measure of men's actual threat potential (derived from measures of their upper-body strength, height, and weight) and composite measures of these men's perceived facial and vocal threat potential (derived from dominance, strength, and weight ratings of their faces and voices, respectively). Although men's perceived facial and vocal threat potential were positively correlated, men's actual threat potential was related to their perceived facial, but not vocal, threat potential. Consistent with other recent work on cues of men's threat potential, these results present new evidence that men's faces may be a more valid cue of these aspects of threat potential than their voices are.

Whereas Chapters 2 and 3 arguably focused on the possible role of face shape characteristics in communicating information about physical condition, Chapter 4 focused specifically on facial coloration. In Chapter 4, I investigated the effects of manipulating color cues in White UK and Chinese faces on White UK and Chinese participants' judgments of attractiveness and health. By contrast with the cross-cultural similarity between White UK and Black African participants' responses to facial coloration reported in previous studies, I found cultural differences in the effects of facial coloration on Chinese and White UK participants' facial attractiveness and health judgments. While both Chinese and White UK participants preferred faces with increased lightness and redness, Chinese participants had stronger preferences for lightness and White UK participants had stronger preferences for redness. More

strikingly, while Chinese participants preferred faces with decreased yellowness, White UK participants preferred faces with increased yellowness, and this effect was not qualified by face ethnicity. These results suggest that preferences for facial coloration are not necessarily universal, but can differ across cultures.

The research reported in this thesis suggests that faces contain information about body size (Chapters 2 and 3). They also show that responses to facial color cues, a putative cue of physical condition preferences for which have previously been suggested to be highly similar across cultures, can vary as a function of cultural factors (Chapter 4). Together, these results indicate that, although aspects of physical condition may be reflected in facial appearance, responses to facial cues are not necessarily universal.

Table of Contents

Publication statement.....	i
Abstract.....	ii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
Acknowledgments.....	viii
Author's Declaration	ix
Chapter 1.....	1
General Introduction.....	1
1.1 Seeing Health in the Face	1
1.1.1 Frequency of Illness	2
1.1.2 Immune Function.....	6
1.1.3 Genetic Markers of Health.....	7
1.1.4 Skin Health.....	7
1.1.4 Cardiovascular Health.....	10
1.1.5 Longevity	11
1.2 Facial Appearance and Anthropometrics.....	11
1.2.1 Height.....	11
1.2.2 Weight and Adiposity.....	12
1.2.3 Strength.....	16
1.3 Hormonal Profiles and The Face.....	19
1.3.1 Testosterone	19
1.3.2 Progesterone and Estradiol.....	20
1.3.2 Cortisol	20
1.4 Current Research.....	21
Chapter 2.....	23
Women's facial attractiveness is related to their body mass index, but not their salivary cortisol	23
2.1 Introduction.....	24
2.2 Methods	26
2.3 Results.....	28
2.4 Discussion.....	33
Chapter 3.....	37
Interrelationships among men's threat potential, facial dominance, and vocal dominance	37
3.1 Introduction.....	38
3.2 Methods	39
3.3 Results.....	41
3.4 Discussion.....	44
Chapter 4.....	47
Cultural differences in preferences for facial coloration.....	47
4.1 Introduction.....	48

4.2 Methods	49
4.2.1 Participants.....	49
4.2.2 Stimuli.....	49
4.2.3 Procedure.....	51
4.3 Results	52
4.3.1 Attractiveness judgments and facial yellowness	52
4.3.2 Attractiveness judgments and facial lightness.....	53
4.3.3 Attractiveness judgments and facial redness	54
4.3.4 Effects of facial coloration on health perceptions.....	56
4.4 Discussion	59
Chapter 5.....	62
General Discussion.....	62
5.1 Facial Cues of Hormone Levels	65
5.2 Methodological Contribution	67
5.3 Facial and Vocal Cues of Anthropometric Profile	68
5.4 Cross-Cultural Differences.....	70
5.5 Facial Cues of Health	70
5.6 Conclusion	71
References	72

List of Tables

Table 2. 1 r values (and 2-tailed p values) for linear relationships among all variables.	29
Table 3. 1 Inter-correlations among test sessions for each trait.	41
Table 3. 2 Inter-correlations among all individual variables.....	43

List of Figures

Figure 1. 1 Women’s BMI and facial features.....	15
Figure 1. 2 Men’s strength and facial features.....	17
Figure 1. 3 Strength and 3D faces.....	18
Figure 2. 1 Scatterplots showing relationships between women’s BMI and each facial dimension.....	30
Figure 2. 2 Scatterplots showing relationships between women’s average cortisol (standardized for time of day) and each facial dimension.....	31
Figure 2. 3 Scatterplots showing relationships between cortisol from first test session (standardized for time of day) and each facial dimension.....	32
Figure 4. 1 Examples of Chinese and White UK male face stimuli used in our study. ..	51
Figure 4. 2 Attractiveness judgments and facial yellowness.....	53
Figure 4. 3 Attractiveness judgments and facial lightness.....	54
Figure 4. 4 Attractiveness judgments and facial redness.....	56
Figure 4. 5 Health Judgments and facial yellowness.....	57
Figure 4. 6 Health judgments and facial lightness.....	58
Figure 4. 7 Health judgments and facial redness.....	59

Acknowledgments

I would like to thank Ben Jones and Lisa DeBruine for their supervision. I really enjoyed being your student and a member of the lab family.

I would also like to thank all lab members for your friendship and knowledge. I feel extremely lucky to have worked with you all.

I would like to thank my parents and my sister Fei who give me emotional help so that I have no fear to face any challenge in my life.

Last but not least, I would like to thank every special person that makes my PhD life bright.

Author's Declaration

I, Chengyang Han, hereby certify that this thesis is my original work that is carried out under the normal terms of supervision, and it has not been submitted in any previous application for a higher degree.

Date:

Signature:

Chapter 1

General Introduction

The human face has been extensively studied, since it conveys a great deal of information that is important for social interaction (for reviews, see Adolphs, 2001; Emery, 2000; Haxby, Hoffman, & Gobbini, 2000). Facial appearance plays an important role in fundamental aspects of human behavior, such as mate choice (e.g. DeBruine, et al., 2010; Jones et al., 2004, 2007; Little, Jones, & DeBruine, 2011; Wincenciak et al., 2015). Social perceptions of facial appearance may reflect psychological adaptations to identify underlying physiology of individuals (e.g., Buss & Schmitt 1993; Johnston, 2006). For example, facial attractiveness may be positively correlated with individual health status and fertility (e.g., Folstad & Karter, 1992; Little, Jones, DeBruine, & Feinberg, 2008) and facial dominance may be linked to aspects of physical condition (e.g., body size and strength) that allow for high resource-holding ability (e.g., Thornhill & Gangestad, 1993, 1999; Krupp, DeBruine, & Jones, 2011). Studying the underlying physiology behind facial appearance can then help build understanding of these aspects of human behavior.

In this chapter, I will first review previous research on the potential links between facial appearance and aspects of health. Next, I will discuss previous research on the potential links between anthropometric attributes (i.e. height, weight and strength) and facial appearance. Finally, I will briefly discuss the literature on facial appearance and fertility and health-related hormones (i.e. testosterone, progesterone, estradiol, and cortisol).

1.1 Seeing Health in the Face

Evolutionary speaking, it is advantageous to bond with healthy mates and cooperate with healthy individuals, especially for people in the geographical areas carrying relatively greater prevalence of pathogens (Gangestad & Buss, 1993). It has been suggested that selecting a healthy mate can provide many benefits. These include both biological advantages, such as increased fertility, disease avoidance, and good genes for offspring, and material advantages, such as better parenting, nutrition, and protection (Andersson, 1994). Moreover, healthy

individuals tend to function well and potentially live longer, which means they could stably bring resources to benefit their mates, offspring and allies, over a longer period of time, whereas unhealthy individuals might not survive to reciprocate one's aid (Thornhill & Gangestad, 1993, 1999; Krupp, DeBruine, & Jones, 2011).

Humans may have evolved an ability to assess health status from facial cues to avoid contagion and pathogen, improving survival chances (Zebrowitz & Rhodes, 2004). In the past decades, many studies have been conducted in western societies to investigate perceived facial cues that are related to actual health (e.g. Honekopp et al., 2004; Roberts et al., 2005b). However, results are very mixed. Studies employed various approaches to evaluate human health, such as frequency of illness, genetic markers of health, immune function, skin health, cardiovascular health, and longevity (e.g. Boothroyd et al., 2013; Foo, Rhodes, & Simmons, 2017; Hönekopp et al., 2004, 2007; Kalick et al., 1998; Lie, Simmons, & Rhodes, 2010; Rantala et al., 2012, 2013a, 2013b; Re et al., 2015; Thornhill & Gangestad, 2006). I will now discuss these studies.

1.1.1 Frequency of Illness

In this section, I will discuss studies investigating possible links between reported frequency of illness and facial appearance, grouped by the aspects of facial appearance that they studied: 1) Facial attractiveness, facial health and facial adiposity, 2) Facial symmetry and facial averageness, 3) Facial sexual dimorphism.

1.1.1.1 Facial Attractiveness, Facial Health and Facial Adiposity

Facial Attractiveness

Kalick et al. (1998) used the Intergenerational Studies of Development and Aging database (a set of face images and health data collected from a sample of participants born between 1920 and 1929) to investigate the relationship between facial attractiveness and health. Health was measured from doctors' ratings of general health based on medical records. Both male and female participants' photos were taken during adolescence. No relationships were found between adolescent facial attractiveness and health conditions during any age periods (Kalick et al., 1998). However, some researchers have criticized this study because it used unstandardized black and white face faces, in which potential health cues

may be absent or obscured. For example, variation in facial expressions and lack of color information could have masked cues of health (Buechner, Maier, Lichtenfeld, & Elliot, 2015; Rhodes et al., 2001; Stephen, Smith, Stirrat, & Perrett, 2009; Zebrowitz et al., 2014).

Apart from relationships between facial appearance and general health condition, other studies have investigated possible relationships between facial appearance and specific illnesses (Shackelford et al., 1999; Gray et al., 2012; Boothroyd et al., 2013). For example, Shackelford et al. (1999) found that, in female participants, headache frequency was negatively correlated with facial attractiveness. In male participants, both sore throat or cough and runny or stuffy nose were negatively correlated with facial attractiveness (Shackelford et al., 1999). However, these correlations would not be significant if corrected for multiple comparisons. Gray et al. (2012) and Boothroyd et al. (2013) found that antibiotic use and frequency of colds or flu was negatively correlated with facial attractiveness in both men and women. Together, the results described above present some evidence for associations between frequency of illnesses and facial attractiveness. However, these relationships do not appear particularly robust, since those significant correlations between illness symptoms and facial appearance were only a small part of large numbers of multiple correlations, which may be false positive results (Boothroyd et al., 2013; Gray et al., 2012; Shackelford et al., 1999).

Perceived facial health and facial adiposity

Kalick et al. (1998) claimed that health cues on faces were obscured by facial attractiveness. Consistent with this proposal, they found that perceived facial health was correlated with actual health when controlling for the effects of facial attractiveness. However, in non-clinical samples, almost all attempts to replicate this pattern of results have been unsuccessful, with none of the studies observing this pattern of correlations (Boothroyd et al., 2013; Gray et al., 2012; Kramer et al., 2012). By contrast, several recent studies have found that people perceived to have lower levels of facial adiposity report fewer past health problems, score higher on measures of cardiovascular health, and tend to live longer (Coetzee et al., 2009; Reither et al., 2009; Tinlin et al., 2013). These results suggest that facial adiposity may be a particularly reliable facial health cue.

2.1.1.2 Facial Symmetry and Facial Averageness

Symmetry

Fluctuating asymmetry (FA) is deviation of morphologic symmetry in bilaterally paired traits and is thought to signal individual development under disruptive effects of both environmental pressures (e.g., parasitism, pollution) and genetic stress (e.g., mutations, inbreeding; Little, Jones, & DeBruine, 2011; Møller, 1997; Møller & Swaddle, 1997; Møller & Thornhill, 1998; Thornhill & Møller, 1997). Although controversial (e.g. Rhodes et al., 2001; Thornhill & Gangestad, 2006; Pound et al., 2014), FA has been suggested as a potentially valuable cue of individual developmental stability and, therefore, health (Kowner, 1996; Livshits & Kobylanski, 1991; Simmons, Rhodes, Peters, & Koehler, 2004).

Symmetric faces are preferred for both attractiveness judgments and health judgments (Rhodes et al., 1998; Perrett et al., 1999; Little & Jones, 2003; Little & Jones, 2006; Little, Apicella, Marlowe, 2007; Waitt & Little, 2006; Rhodes et al., 2007). However, while there is good evidence that facial symmetry looks attractive and healthy, evidence that it is linked to measures of actual health is mixed.

Rhodes et al. (2001) employed both subjective ratings of facial symmetry and objective measurement through facial metric analyses of position of eyes, nose, mouth, cheekbones, and jaw. They found little evidence for an association between actual health and symmetry, other than a marginally significant correlation between measured female facial asymmetry and health in middle adulthood. Other studies that focused on facial symmetry and frequency of illness mostly assessed facial symmetry using similar facial metric methods (Hönekopp, Bartholomé, & Jansen, 2004; Hume & Montgomerie, 2001; Shackelford & Larsen, 1997; Thornhill & Gangestad, 2006). Among these studies, only Thornhill and Gangestad (2006) found positive associations between facial FA and health that indexed by number of respiratory infections in the past. Although Shackelford and Larsen (1997) reported a few weak associations between facial asymmetry and self-reported health symptoms (including mental health), they looked at a very large number of specific symptoms and more than 1000 correlations were examined, obviously raising the probability of false positives. Consequently, their results should be

treated very cautiously (Luevano, 2007). Additionally, negative results (i.e. non-significant) were found in one recent study with a particularly large sample (N=4732), with health assessed since childhood (Pound et al., 2014). This latter study supports the proposal that links between facial symmetry and actual health reported in some previous work were most likely false positives. Indeed, meta-analyses have also cast doubt on the robustness of the hypothesized link between FA and health in nonhuman animals (Polak, 2003; Tomkins & Simmons, 2003).

Averageness

Facial averageness (or prototypicality) is defined as how closely a face resembles the majority of other faces within a population (Little et al., 2011). The first visual representation of an average face was created by Francis Galton (1878), who also found that composited average faces were more attractive than individual faces (Galton, 1879). Other more recent studies have replicated this pattern of results (Grammer & Thornhill, 1994; Jones et al., 2001, 2004; Penton-Voak et al., 2001; Scheib et al., 1999). Although one study found that facial distinctiveness, the converse of facial averageness, was negatively related to past general health condition (Rhodes et al., 2001), more evidence is needed to support a relationship between facial averageness and frequency of illness.

1.1.1.3 Facial Sexual Dimorphism

Facial sexual dimorphism are mature features in adult human faces that differ between males and females. These are thought to reflect the circum-pubertal masculinization and feminization of males and females (Enlow, 1982; Thornhill & Møller, 1997; reviewed in Little et al., 2011). For example, males tend to have large jawbones, high brow ridges, thin cheeks, and prominent cheekbones, which make them look masculine (Enlow, 1982; Thornhill & Møller, 1997; reviewed in Little et al., 2011). Females tend to have smaller jaws, brow ridges and cheekbones, and larger lips (Enlow, 1982; Thornhill & Møller, 1997; reviewed in Little et al., 2011).

Facial Masculinity

Rhodes et al. (2003) found rated masculinity in adolescent male faces correlated with their perceived health and actual health based on detailed medical

examinations and health histories. Although these correlations were still significant when controlling for attractiveness, attractiveness was not correlated with either masculinity or perceived health. Thornhill and Gangestad (2006) found male facial masculinity was negatively correlated with respiratory disease and antibiotic use, but not stomach illness. Additionally, there is evidence suggesting that male facial masculinity is positively linked to developmental health, as indexed by body fluctuating asymmetry (Gangestad & Thornhill, 2003). Consistent with Thornhill and Gangestad (2006), Boothroyd et al. (2013) also found male facial masculinity was negatively associated with respiratory diseases, but not stomach illness. Additionally, Boothroyd et al. (2013) found that male facial masculinity positively predicted future respiratory illness, but not links to antibiotic use. Although some aspects of these studies' results were inconsistent with each other, each found some evidence that male facial masculinity positively links to health.

Facial Femininity

Thornhill and Gangestad (2006) found female facial masculinity was positively correlated with self-reported respiratory infections, but not stomach and intestinal infections or antibiotic use. Similarly, Gray and Boothroyd (2012) found female facial femininity was negatively linked with flu and antibiotic use, but not stomach bugs. Koehler, Simmons, Rhodes and Peters (2004) found positive associations between female facial femininity and body FA, but not facial FA. By contrast, Gangestad and Thornhill (2003) found a curvilinear relationship, but not a linear correlation, between women's femininity and facial FA, but not body FA. Furthermore, Rhodes et al. (2003) found no correlation between rated female facial femininity and actual health, although facial femininity was positively correlated with perceived health.

1.1.2 Immune Function

Four empirical studies have investigated possible relationships between facial traits and immune responses (Rantala et al., 2012, 2013a, 2013b; Skrinda et al., 2014). They found that, in male samples, levels of immune response were positively associated with male facial attractiveness and facial masculinity and negatively associated with male facial adiposity (Rantala et al., 2012, 2013b; Skrinda et al., 2014). However, in female samples, facial attractiveness and levels of immune

response were not linked (Rantala et al., 2013a). Using a wider range of immune responses, another more recent study also observed no evidence that facial appearance predicted immune function in either males or females (Foo et al., 2017a). This more recent study suggests the links between immune response and male facial appearance reported previously are not robust.

1.1.3 Genetic Markers of Health

MHC genes code for peptides that initiate immune response. As each MHC allele corresponds to a restricted range of antigens, large MHC genetic diversity (i.e. MHC heterozygosity) could provide resistance to a broad range of pathogens (reviewed in Lie, 2009; Suri et al., 2003; Penn, 2002; Doherty & Zinhermagel, 1975). Consequently, individuals with greater MHC heterozygosity should have the ability to avoid more illness (i.e. their immune system can successfully detect and respond to a larger range of pathogens, Apanius et al., 1997). Male facial attractiveness is positively linked to MHC heterozygosity (Lie, Rhodes, & Simmons, 2008; Lie, Simmons, & Rhodes, 2010; Roberts et al., 2005b), but no links were found between female facial attractiveness and MHC heterozygosity (Coetzee et al., 2007; Lie, Rhodes, & Simmons, 2008; Lie, Simmons, & Rhodes, 2010). However, Lie et al. (2010) found MHC dissimilarity was associated with female facial attractiveness, but not male facial attractiveness. Thornhill et al. (2003) did not find any links between facial attractiveness and MHC heterozygosity in either sex. Thus, evidence for links between attractiveness and heterozygosity is mixed.

1.1.4 Skin Health

Recent studies have investigated possible effects of facial skin color cues on attractiveness and health judgments. Research has suggested that the effects of skin coloration on facial attractiveness and health judgments are at least as large as effects of shape cues (e.g., Stephen et al., 2012b; Said & Todorov, 2011; Pound, Stephen, Clark, & Penton-Voak, 2010; Torrance, Wincenciak, Hahn, DeBruine, & Jones, 2014).

The CIELab color space (CIE, 1976) is the most widely used color space in facial skin color research. It is modeled on the human visual system and consists of three independent color axes: L* (luminance-dark), a* (red-green) and b* (yellow-blue). It

has been reported that increasing facial yellowness, lightness, or redness increases both attractiveness and perceptions of traits that are highly correlated with attractiveness, such as health (Fisher, Hahn, DeBruine, & Jones, 2014; Kandrik et al., 2017; Stephen, Law Smith, Stirrat, & Perrett, 2009a; Stephen, Coetzee, Smith, & Perrett, 2009b; Stephen, Coetzee, & Perrett, 2011; Lefevre, Ewbank, Calder, Von Dem Hagen, & Perrett, 2013). Indeed, facial skin color is not only associated with perceived health, but also related to aspects of human health that can be modulated by lifestyle (e.g. diet, sun exposure).

Skin Yellowness

Carotenoids are a group of yellow-red pigments that are contained in a variety of vegetables and fruits. Modestly increasing carotenoids contained in vegetables and fruits can make facial skin color increase in yellowness (Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012; Tan, Graf, Mitra, & Stephen, 2015; Foo, Rhodes, & Simmons, 2017). One study also found that skin yellowness (CIELab b*) was positively correlated with levels of carotenoids in the skin, and suggested this was attributable to normal dietary intake (Alaluf, Heinrich, Stahl, Tronnier, & Wiseman, 2002).

Apart from being a color ornament, carotenoids play an important role in disease resistance and immunocompetence in humans (reviewed in Stephen, 2009). For example, β -carotene (one forms of carotenoids) supplementation elevates the active number of T lymphocytes in healthy human adults (Alexander, Newmark, & Miller, 1985), and has a positive influence on the growth of the thymus gland in children (Seifter, Rettura, & Levenson, 1981). Additionally, β -carotene levels have been negatively correlated to skin cancer, photoaging of the skin (Stahl, Heinrich, Jungmann, Sies, & Tronnier, 2000; Taylor, Stern, Leyden, & Gilchrest, 1990) and incidence of UV-induced erythema (Alaluf et al., 2002), which may be because of its antioxidative properties (Alaluf et al., 2002).

The carotenoid trade-off hypothesis proposed that using carotenoids for coloration prevents their use by the immune system (Von Schantz, Bensch, Grahn, Hasselquist, & Wittzell, 1999; Lozano, 1994). Carotenoid ornamentation (i.e. skin yellowness) may therefore be an honest signal of health (Lozano, 1994).

Exceptionally, unusually high levels of carotenoids, however, can occur in the body, either due to pathological mechanisms such as a failure to convert carotenoids to vitamin A or excessive intake. This can lead to skin yellowing, and is known as carotenaemia (Monk, 1983).

Overall, high levels (in normal range) of carotenoids are therefore associated with elevated health status and increased facial skin yellowness, which could be caused by increased vegetables and fruits consumption in diet. In other words, individuals' facial yellowness increasing may due to increase consumption of vegetables and fruits in their diet, which potentially signals their general health improvement. As indirect evidence, facial skin yellowness is positively correlated with facial attractiveness (which is highly correlated with perceived facial health) in both white and black African populations (Coetzee, Greeff, Stephen, & Perrett, 2014). Although one recent study suggested that carotenoid-based coloration may not be an honest signal of health (oxidative stress, innate immune function and semen quality were tested), they only tested on White male with beta-carotene (i.e. only one form of carotenoids) supplementation (Foo et al., 2017).

Skin Lightness

Skin lightness is negatively correlated with ultraviolet ray exposure. This tanning response causes increased darkness of the skin and increases levels of melanin. Melanin mainly affects levels of luminance (L*) and yellowness (b*) on the CIElab axes, showing a dark yellow colour (Stamatas, Zmudzka, Kollias, & Beer, 2004). Melanin is an effective absorber of light and can dissipate ultraviolet radiation efficiently (Meredith & Riesz, 2004), which can protect DNA and proteins from ultraviolet ray damaging, avoiding skin cancer and sunburn (Daniels, van der Leun, & Johnson, 1973; Robins, 1991). However, the prevention of ultraviolet penetration into the deep skin also prevents the formation of vitamin D that is mainly obtained from sunlight stimulation in the derma (Loomis, 1976). Vitamin D deficiency can lead to osteomalacia in adults and rickets in children (Murray, 1934). Therefore, skin luminance can be reduced due to sunlight exposure, which can protect skin damage from ultraviolet ray reducing skin cancer chance, but can also lead to vitamin D deficiency. Recent studies found that facial lightness is positively linked to facial attractiveness judgments (Stephen et al., 2009a, 2009b, 2011), though

there are cultural differences in degrees of skin lightness preference that may be caused by mass media exposure (Xie & Zhang, 2013).

Skin Redness

Skin redness can be affected by blood perfusion in blood vessels close to the surface of the skin (Stephen et al., 2009b). It has been suggested that increasing red skin coloration increases facial attractiveness and perceived health (Stephen et al., 2009a, 2009b; Re et al., 2011; Whitehead et al., 2012a, 2012b), which are thought to primarily reflect responses to facial cues of cardiovascular health (Stephen et al., 2009b).

On the other hand, it has been observed in animal species (e.g. female rhesus macaques and mandrills) that estradiol can increase skin redness, which may be a cue of fertility (Dixson, 1998; Dubuc et al., 2009; Setchell et al., 2006). In women, Jones et al. (2015) observed that women's facial skin was redder when their estradiol levels were higher and Oberzaucher et al. (2012) found women's facial redness increased on the period of ovulation, when estradiol and fertility are both high. These data suggest that changes in facial redness of women might contain information about their general fertility, and reflect the possible vasodilatory effects of estradiol (Sobrino et al., 2009).

1.1.4 Cardiovascular Health

Cardiovascular health is an important element to individual health and physical fitness. It is related to almost all sports performance. There are four studies that investigated the relationship between facial traits and physical fitness using cardiovascular related data as evidence (Hönekopp, Bartholomé, & Jansen, 2004; Hönekopp, Rudolph, Beier, Liebert, & Müller, 2007; Shackelford & Larsen, 1997; Shackelford & Larsen, 1999). Hönekopp et al. (2004, 2007) used the Haro fitness test, which involves running, sit ups, push ups, etc. Results show that there is positive correlation between physical fitness test performance and attractive facial traits, in females, but not males. Shackelford & Larsen (1997, 1999) also assessed cardiovascular health (cardiac recovery time after exercise), finding a link between facial attractiveness and recovery time in male participants, but not in female participants. Overall, data suggests links between facial attractiveness and

cardiovascular health in both males and females, though the results were inconsistent across studies.

1.1.5 Longevity

Face researchers have investigated whether there are facial cues that predict the general longevity of individuals (Abel & Kruger, 2010; Christensen et al., 2009; Re et al., 2015; Henderson & Anglin, 2003). Two of these employed past yearbook photographs of students in the 1920s (Re et al., 2015; Henderson & Anglin, 2003), which means all the facial photos were taken in those people's school age (i.e. young adults). Henderson and Anglin (2003) found that facial attractiveness of those young adults in photos was positively correlated with their actual longevity and the prediction was more robust for male faces than female faces. Re et al. (2015) did not replicate the association between facial attractiveness and longevity. However, they found facial adiposity was negatively correlated with longevity and many studies have reported that facial adiposity has a strong negative correlation with facial attractiveness (Coeztee et al., 2009). In conclusion, facial traits, such as facial attractiveness and facial adiposity, may be used as a predictor of longevity even for young adults.

1.2 Facial Appearance and Anthropometrics

1.2.1 Height

Human body height has been found to play an important role in social inference and mate choice (reviewed in Re & Perrett, 2012). It has been suggested that taller people typically have higher income (Meyer & Selmer, 1999; Rashad, 2008; Steckel, 1983) and are likely to obtain greater success in business and political careers (Judge & Cable, 2004; McCann, 2001; Murray & Schmitz, 2011; Sorokowski, 2010). In a mating context, male body height is desirable in speed-dating events (Kurzban & Weeden, 2005) with taller men being more likely to receive interest from women in personal advertisements (Pawlowski & Koziel, 2002). Although high stature increases male mating advantage (Shepperd & Strathman, 1989), evidence for associations between female statures and mating advantage are mixed (Courtiol et al., 2010; Shepperd & Strathman, 1989; Swami et al., 2008).

Given that tall people are generally preferred in mate selection, there may be cues in faces that signal body height. Indeed, body height is positively correlated with head size (Geraedts et al., 2011), face size (Mitteroecker, Gunz, Windhager, & Schaefer, 2013), and perceived facial height (Burton & Rule, 2013; Re et al., 2012; Re et al., 2013; Schneider, Hecht, Stevanov, & Carbon, 2013). It was suggested that individual levels of testosterone influence the facial appearance and body height during growth (Lorentzon, Swanson, Andersson, Mellstrom, & Ohlsson, 2005; Verdonck, Gaethofs, Carels, & de Zegher, 1999).

Moreover, people with long faces were perceived to be tall. Re and Perrett (2012) found that increasing facial length in photos could cause targets to be perceived taller. Facial elongation (full length of the face divided by the full width), but not facial width-to-height ratio, also predicted perceived height (Re et al., 2013). Additionally, chin area was found as a unique physical mediator of the actual-perceived height association, suggesting that individuals with large chins tend to be perceived as taller (Burton & Rule, 2013).

Furthermore, the relationship between perceived height from face and actual body height is partially mediated by targets' facial maturity and dominance, suggesting that social perceptions could influence estimations of height. Indeed, targets with higher perceived social status are judged as physically taller (Koulack & Tuthill, 1972) and political candidates who are perceived as taller are more likely to be favored by voters (Sorokowski, 2010).

1.2.2 Weight and Adiposity

Body weight influences our social life and health. For example, in western society, socio-economic status and body weight tend to be negatively correlated (e.g., Moore, Stunkard, & Srole, 1997) and romantic partners' weights are positively correlated (reviewed in Fisher et al., 2014). Obese individuals, especially during adolescence, often encounter negative labels, such as lazy, stupid, less attractive, or having few friends, and they are also vulnerable to weight biases, negative stereotypes, and stigmatization from others (Puhl & Latner, 2007). These negative

attitudes and stigma can negatively impact individuals' psychological and physical health (Puhl & Latner, 2007).

Body Mass Index (BMI) is weight scaled for height, which is frequently employed by health professionals and research scientists to measure adiposity (e.g. Stommel & Schoenborn, 2010; Jia & Lubetkin, 2005). It provides a simple numeric measure of a person's thickness or thinness. In other words, it quantifies the amount of tissue mass (fat, muscle, and bone) of individuals so that people can compare weight/adiposity levels objectively, with little artificial influence from height differences. The World Health Organization (WHO; WHO, 2000) generally classifies adults' BMI under 18.5 kg/m² as underweight, between 18.5 kg/m² and 25 kg/m² as normal weight, between 25 kg/m² and 30 kg/m² as overweight, and over 30 kg/m² as obese.

A large number of studies have suggested that individuals in unhealthy ranges of BMI have increased risk of developing health problems. For example, compared to normal weight adults, underweight adults have decreased vitality, decreased immunity, poorer mental health, increased use of health services, and increased mortality (Brown et al., 2000; Flegal et al., 2005; Ritz and Gardner, 2006); overweight and obese adults have high risk of respiratory problems, osteoarthritis, gout, stroke, coronary artery disease, gallbladder disease, diabetes mellitus, sleep apnea, and a variety of cancers (Pi-Sunyer, 1993; Manson et al., 1995; Must et al., 1999; Brown et al., 2000; Wilson et al., 2002; Mokdad et al., 2003). Moreover, BMI was also associated with both men's and women's fertility health (e.g., Jokela, Elovainio, & Kivimäki, 2008; Pandey, Pandey, Maheshwari, & Bhattacharya, 2010; Sallmén, Sandler, Hoppin, Blair, & Baird, 2006).

Additionally, it has been suggested that the associations between BMI and health risks in Asian descendants is different from European descendants. Asians have a higher risk of type 2 diabetes and cardiovascular disease at lower BMIs than the WHO cut-off point for overweight, 25 kg/m², though the cutoff points for observed risk varies among different Asian populations (Barba, Cavalli-Sforza, Cutter, & Darnton-Hill, 2004).

Given that weight is associated with health and our social life, can we easily and accurately judge others' weight without scale? Face is one of the most direct and approachable information we can see from others, and it is an important cue that we are using to evaluate one's weight condition. Windhager, Patocka and Schaefer (2013) using geometric morphometric methods found that white female adolescents with high BMI tend to have relatively large lower face with a wide jaw, small eyes with flat and low eye brows, wide and short nose, and full lips with the corners of a narrow mouth downturned (Figure 1.1 from Windhager et al., 2013). Apart from face shape, Mayer, Windhager, Schaefer, and Mitteroecker (2017) found women with higher BMI had a brighter and more reddish skin color than women with lower BMI. Similar patterns of results (i.e. both face shape and face color convey BMI information) were found in large samples (524 White female) with data driven approach (Wolffhechel et al., 2015). Henderson, Holzleitner, Talamas, and Perrett (2016) using 3D face models generated estimated BMI merely from face, which were highly correlated with actual BMI, which suggests face shape shows cues of BMI.

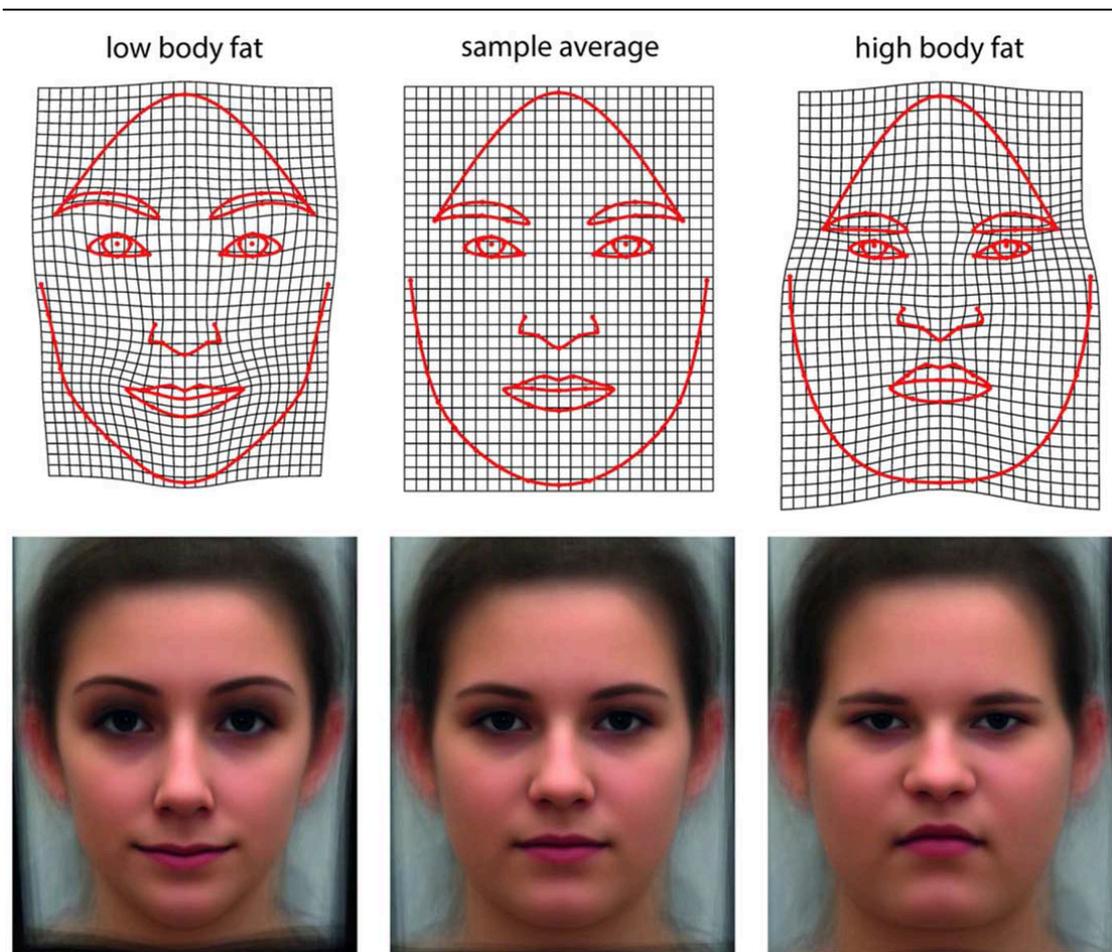


Figure 1. 1 Women's BMI and facial features. High BMI White female adolescents facial features are associated with a relatively large lower face with a wide jaw, small eyes with flat and low eyebrows, wide and short nose, and full lips with the corners of a narrow mouth downturned. From Windhager et al. (2013).

The above four studies only tested White females, but all the results suggest that faces do convey body weight information (e.g. BMI; Henderson et al., 2016; Mayer et al., 2017; Windhager et al., 2013). Then, next questions are: Can people judge other's weight merely from targets' face, and is this universally true? Indeed, people tend to judge others' weight from targets' face. Facial adiposity, which is the perceived weight from face, is positively and linearly correlated with BMI (e.g. Coetzee, Perrett, & Stephen, 2009; Tinlin et al., 2013).

There is growing evidence that facial adiposity is not only related to adults' health at the perceptual level (Coetzee, Re, Perrett, Tiddeman, & Xiao, 2011; Coetzee, Perrett, & Stephen, 2014; Fisher, Hahn, Debruine, & Jones, 2014), but also to actual health condition, such as respiratory health (e.g. cold), cardiovascular health (e.g. blood pressure; Coetzee, Perrett, & Stephen, 2014), general physical and

psychological health (Tinlin et al., 2013), and immune response (e.g. the antibody response to a hepatitis C vaccination; Rantala et al., 2013b). Moreover, neck adiposity has been shown to be a better discriminatory factor in identifying type 2 diabetes than BMI (Tafeit, Moller, Pieber, Sudi, & Reibnegger, 2000) and neck circumference has been shown to be a significant predictor of hypertension, independent of BMI (Laakso, Matilainen, Keinanen-Kiukaanniemi, 2002). Additionally, cheek fat has been found to be related to visceral abdominal fat, which is thought to be a particularly risky place to carry excess weight, though the participants in this study were all clinic patients (Levine, Ray, & Jensen, 1998).

In conclusion, there is evidence that BMI and facial adiposity are positively correlated and both of them are associated with health. However, the cross ethnicity condition can significantly impact these relationships (except a few studies tested relationships between facial adiposity and health condition in different ethnicity populations), especially in Asia and White populations (e.g. Barba, Cavalli-Sforza, Cutter, & Darnton-Hill, 2004; Schneider, Hecht, Stevanov, & Carbon, 2013). Therefore, future research should consider ethnicity factor when conduct facial adiposity and BMI related studies. Meanwhile, researchers could also include neck adiposity as a factor.

1.2.3 Strength

Strength is related to aspects of physical fitness, such as health (longevity), and formidability (physical competition advantage). It was found that handgrip strength is the best predictor of human longevity, compared to other physical indexes (e.g. blood pressure and physical activity levels), in a multi-countries population longitudinal study (Leong et al., 2015). One the other hand, obviously, in physical competition (e.g. physical fighting), large strength is advantageous (i.e. formidability).

A growing body of literature suggests that intrasexual selection pressures might play an important role in shaping face traits (Puts, 2010; Puts, Jones, & DeBruine, 2012; Scott, Clark, Boothroyd, & Penton-Voak, 2013; Holzleitner & Perrett, 2016). Great strength can directly benefit intrasexual competition (e.g. fighting). Therefore, it may have shaped the development of certain facial traits that signal physical

strength. Windhager, Schaefer, and Fink (2011) found men with larger handgrip strength had a rounder face with a lower forehead, widening between eyebrows, shorter nose, broadening of lower face and pounced masseter region (jaw muscles), using 2D images (Figure 1.2 from Windhager et al., 2011). Holzleitner and Perrett (2016) using 3D face images found that greater strength is associated with male facial features, such as higher forehead, more widely spaced eyebrows and eyes, greater bizygomatic width (more pronounced cheekbones), a longer midface, a wider mouth and a narrower mandible. Regarding females, higher strength had a shorter forehead, lower brow height and smaller, deeper-set eyes, a shorter middle range of face, a wider nose and mouth with thinner lips, shorter and wider chin and a wider and more angular mandible (Figure 1.3 from Holzleitner & Perrett, 2016).

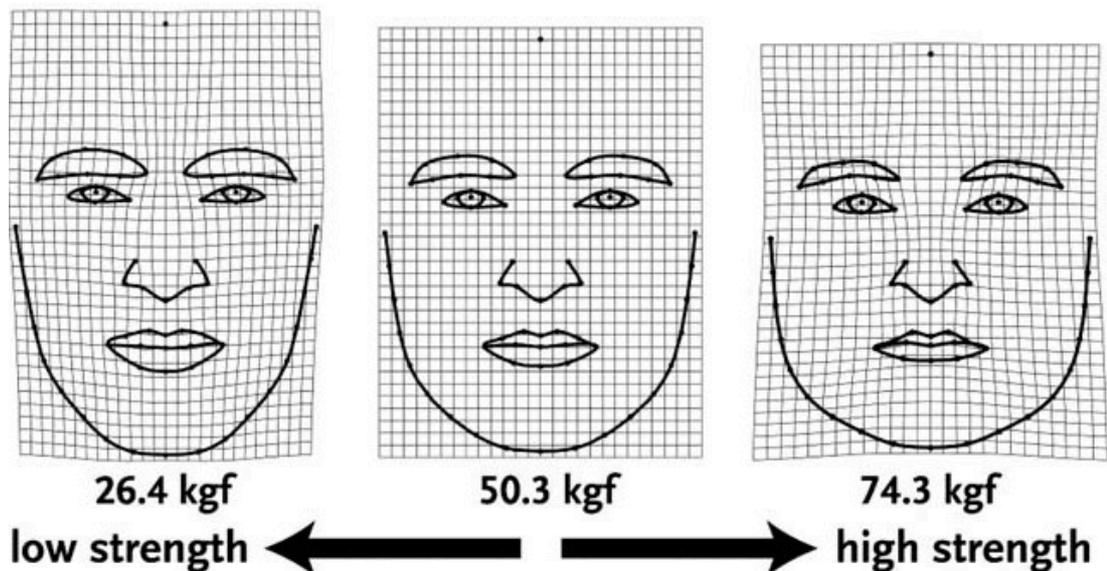


Figure 1. 2 Men's strength and facial features. Men with larger handgrip strength had rounder face with a lower forehead, widening between eyebrows, shorter nose, broadening of lower face and pounced masseter region (jaw muscles). From Windhager et al. (2011).

Actual Strength

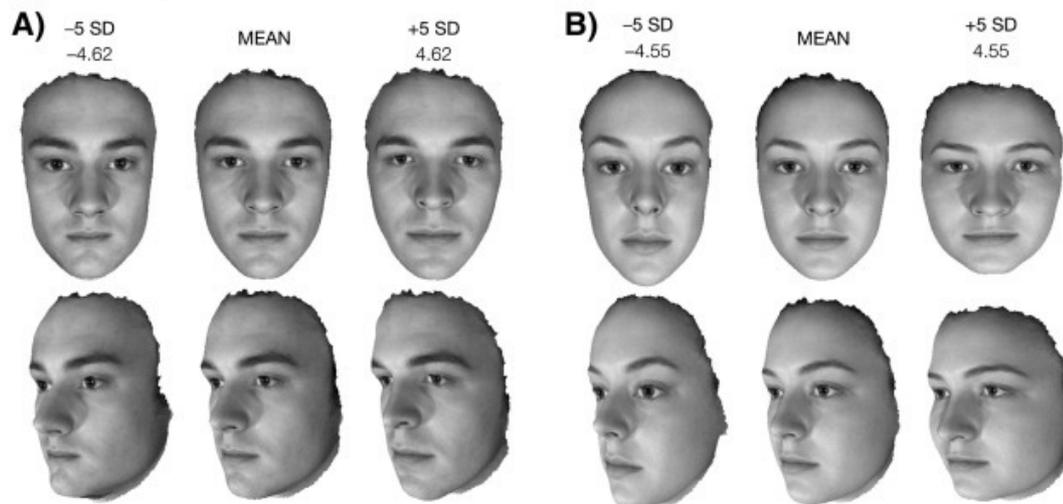


Figure 1.3 Strength and 3D faces. A) Men's strength and 3D faces. Increasing strength is associated with males facial features that are higher forehead, more widely spaced eyebrows and eyes, greater bizygomatic width (more pronounced cheekbones), a longer midface, a wider mouth and a narrower mandible. B) Women's strength and 3D faces. In female, higher strength had a shorter forehead, lower brow height and smaller, deeper-set eyes, a shorter middle range of face, a wider nose and mouth with thinner lips, shorter and wider chin and a wider and more angular mandible. From Holzleitner and Perrett (2016).

As we see, there are a few difference and even contradicted facial features (e.g. lower forehead vs. higher forehead) that signal male strength between results from Windhager et al. (2011) and results from Holzleitner and Perrett (2016). The causes may be from different face images (2D vs. 3D), different facial landmarks, and different techniques (geometric morphometric toolkit vs. Morphanalyser 2.4) that generate difference between high strength and low strength prototype faces.

In order to make advantageous decisions about when to defer and to persevere in conflicts, people may benefit from being able to make accurate assessment of individual differences in aggressive formidability (Sell et al., 2009). Thus, people may have developed the ability to accurately assess physical strength from targets' faces. Indeed, a number of empirical studies have been shown that people can judge individuals' strength from their face (e.g. Holzleitner & Perrett, 2016; Sell et al., 2009; Toscano, Schubert, & Sell, 2014). Sell et al. (2009) reported results of a positive association between perceived physical strength from face photos and actual upper-body strength, from diverse samples included Bolivian horticulturalists, Andean pastoralists and US college students. Holzleitner and Perrett (2016) using

3D faces also found association between perceived facial physical strength and actual strength, though only had weak relationship, which may be because they used the same average skin texture in 3D face images, whereas Sell et al. (2009) used color 2D face images. It was suggested that facial color also conveys strength information (e.g. Stephen, Oldham, Perret, & Barton, 2012a). Holzleitner and Perret's (2016) sample size and diversity were smaller than Sell et al. (2009), and Sell et al. (2009) tested multiple body strength (e.g. arm curl, abdominal crunch, chest press and super long pull), flexed biceps circumference and a self-report measure of strength in their composite measure of actual strength, whereas Holzleitner and Perrett (2016) only tested handgrip strength and chest strength, which all can potentially cause less robust results.

Furthermore, the correlation between perceived strength from face and actual strength is mediated by a number of facial features. For example, facial hair (beard) can exaggerate facial dominance and facial masculinity (Dixson, Lee, Sherlock, & Talamas, 2017), and both facial dominance and facial masculinity are reported highly correlated with actual strength (Fink et al., 2007; Windhager et al., 2011). Facial width to height ratio (fWHR) was linked to both perceived formidability and actual formidability (reviewed in Geniole, Denson, Dixson, Carré, & McCormick, 2015; Zilioli et al., 2014), and strength is one of the important components in formidability (Sell, 2005). Stephen et al., (2012a) reported skin color, especially redness, is associated with judgments of physical dominance. Therefore, facial hair, fWHR and skin color could be factors that mediated the relationship between perceived strength from faces and actual strength.

1.3 Hormonal Profiles and The Face

1.3.1 Testosterone

Several recent studies have focused on the possible links between testosterone and facial appearance (e.g. attractiveness, dominance; see Little et al, 2011 for a review). Previous studies have investigated the association between testosterone and perceptions of facial appearance particularly in male. Some results suggested that basal testosterone levels are positively associated with male facial traits, such as dominance and attractiveness (Penton-Voak & Chen, 2004; Roney et al., 2006;

Swaddle & Reiersen, 2002; Moore et al., 2011a; Roney et al., 2016). However, other studies did not observe these links between basal testosterone levels and male facial attractiveness and dominance-related judgments (Hönekopp et al., 2007; Kandrik et al., 2017; Neave, Laing, Fink, & Manning, 2003; Pound, Penton-Voak, & Surridge, 2009). In female populations, Wheatley et al. (2014) observed a negative association between testosterone and facial attractiveness, but Gonzalez-Santoyo et al. (2015) found there were no links between testosterone and facial attractiveness.

Inconsistent results for testosterone may be due to these correlations being modulated by cortisol (e.g. Moore et al, 2011a,b; Rantala et al., 2012). However, the strongest test of this hypothesis to date saw no evidence of this (Kandrik et al., 2017).

1.3.2 Progesterone and Estradiol

Law Smith et al. (2006) found that facial attractiveness related traits (i.e. femininity, attractiveness, health and the component from these three traits) were positively correlated with late follicular estradiol and positively correlated (marginally significant) with average progesterone levels in luteal phase. However, neither Puts et al. (2013) nor Jones et al. (2017) replicated these results.

1.3.2 Cortisol

Cortisol plays a complex and important role in regulating the immune system (reviewed in Martin, 2009 and Sapolsky et al., 2000). For example, the first wave of glucocorticoids produced in stress responses have both stimulating and inhibitory effects on immunity (Chrousos, 1995; Reichlin, 1993) and both infectious and noninfectious stressors can trigger immune activation (Harbuz & Lightman, 1992; Morrow et al., 1993). However, this activation is typically relatively short lived (Sapolsky et al., 2000). Where levels of glucocorticoids are elevated for relatively long periods of time, such as days or even weeks, they tend to have immunosuppressive effects, such as inhibition of the synthesis, release, and efficacy of mediators that promote immune reactions (see Martin, 2009; Sapolsky et al., 2000). Thus, high trait (i.e., average) levels of cortisol may be a biomarker for poor health.

Rantala et al. (2013) found plasma cortisol levels were negatively associated with female attractiveness. However, Gonzalez-Santoyo et al. (2015) found saliva cortisol levels were negatively associated with female facial dominance but not attractiveness. For male faces, evidence for links between attractiveness and cortisol are similarly mixed (Kandrik et al., 2017).

1.4 Current Research

As you have seen, evidence for links between aspects of facial appearance and physical condition is far from robust (e.g., hormone and facial appearance). This is surprising, since these links are core to many influential theories of attractiveness (e.g., many popular 'mate-choice' theories). Consequently, in the first two empirical studies, I investigated hypothesized relationships between facial appearance and physical condition.

In Chapter 2, I investigated the possible relationships between aspects of facial appearance (attractiveness, health, dominance) and both adiposity and salivary cortisol in a large sample of young adult women. In Chapter 3, I investigated the hypothesized relationships between aspects of men's threat potential (height, upper-body strength, weight) and facial appearance. To foreshadow the results of these studies, I found that women's faces contained cues of their adiposity, but not cortisol (Chapter 2), and that men's faces contained cues to their threat potential (Chapter 3).

An assumption of much of the research on facial cues of physical condition is that responses to these cues are similar across cultures. This claim has been made particularly strongly recently for responses to facial color cues, which have received a great deal of attention in recent years in the attractiveness literature. Consequently, in Chapter 4, I compared Chinese and White UK participants' preferences for color cues in both Chinese and White UK faces. While cultural similarities in these preferences would support the claim that preferences for these cues reflect culturally invariant responses, cultural differences in responses would

challenge the popular and influential hypothesis that responses to color cues in faces are universal.

Chapter 2

Women's facial attractiveness is related to their body mass index, but not their salivary cortisol

The following chapter is based on work published in *American Journal of Human Biology*.

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(3), 352-355.

Abstract

Although many theories of human facial attractiveness propose positive correlations between facial attractiveness and measures of actual health, evidence for such correlations is somewhat mixed. Here we sought to replicate a recent study reporting that women's facial attractiveness is independently related to both their adiposity and cortisol. Ninety-six women provided saliva samples, which were analyzed for cortisol level, and their height and weight, which were used to calculate their body mass index (BMI). A digital face image of each woman was also taken under standardized photographic conditions and rated for attractiveness. There was a significant negative correlation between women's facial attractiveness and BMI. By contrast, salivary cortisol and facial attractiveness were not significantly correlated. Our results suggest that the types of health information reflected in women's faces include qualities that are indexed by BMI, but do not necessarily include qualities that are indexed by cortisol.

2.1 Introduction

Theories of human mate choice often propose that judgments of others' facial attractiveness are psychological adaptations that identify healthy individuals (see Gangestad & Simpson, 2000 and Little et al., 2011 for comprehensive reviews of these theories). Links between health and facial attractiveness might also be expected because distinguishing between healthy and unhealthy individuals is important for both reducing exposure to infectious diseases (e.g., Tybur & Gangestad, 2011) and identifying social partners who will be able to reciprocate investment of resources (e.g., Krupp et al., 2011).

Although many different theories predict correlations between facial attractiveness and measures of actual health, evidence for such correlations is mixed. For example, although some studies have reported that people with more attractive faces report fewer past health problems (e.g., Hume & Montgomerie, 2001; Shackelford & Larson, 1999), other studies have not observed significant correlations between facial attractiveness and reported health problems (Kalick et al. 1998; Thornhill & Gangestad, 2006). Evidence that facial characteristics that are perceived to be healthy (e.g., facial symmetry and prototypicality) are negatively correlated with reported incidence of past health problems is similarly mixed (Rhodes et al., 2001; Shackelford & Larson, 1997; Thornhill & Gangestad, 2006; Zebrowitz & Rhodes, 2004), as is evidence for correlations between sexually dimorphic facial characteristics and past health problems (Gray & Boothroyd, 2012; Rhodes et al., 2003; Thornhill & Gangestad, 2006). Although it has been reported that men with more masculine or attractive faces showed stronger immune responses to hepatitis B vaccinations, no such link between facial attractiveness and immune response was found for women (Rantala et al., 2012, 2013a, 2013b).

While evidence for correlations between most facial cues and measures of actual health is rather mixed, recent work on facial cues of adiposity is more consistent; people whose faces are perceived to be relatively slim report fewer past health problems, score higher on measures of cardiovascular health, and tend to live longer (Coetzee et al., 2009; Tinlin et al., 2013; Reither et al., 2009). Some work

also suggests that facial cues of adiposity predict some aspects of health even when controlling for the role of BMI (Tinlin et al., 2013), suggesting that facial cues of adiposity are not necessarily redundant with other adiposity markers (e.g., body size and/or shape). Men whose faces are perceived to be relatively slim also show stronger immune responses to hepatitis B vaccinations, even when controlling for the effects of facial masculinity (Rantala et al., 2013a). These findings for health measures and facial cues of adiposity are consistent with research suggesting that measures of adiposity, such as body mass index (BMI), are good predictors of long-term health outcomes (reviewed in Calle et al., 1999).

Cortisol plays an important, but complex, role in regulating the immune system (see Martin, 2009 and Sapolsky et al., 2000 for comprehensive reviews). For example, the first wave of glucocorticoids produced in stress responses have both stimulating and inhibitory effects on immunity (Chrousos, 1995; Reichlin, 1993) and both infectious and noninfectious stressors can trigger immune activation (Harbuz & Lightman, 1992; Morrow et al., 1993). However, this activation is typically relatively short-lived (Sapolsky et al., 2000). Where levels of glucocorticoids are elevated for relatively long periods of time, such as days or even weeks, they tend to have immunosuppressive effects, such as inhibition of the synthesis, release, and efficacy of mediators that promote immune reactions (see Martin, 2009 and Sapolsky et al., 2000). Thus, high trait (i.e., average) levels of salivary cortisol may be a biomarker for poor health.

Some recent studies have reported that men with lower average cortisol have more attractive faces (Moore et al., 2011a, 2011b). Additionally, a recent study reported that women with lower average cortisol have more attractive faces, even when controlling for the effects of adiposity (Rantala et al., 2013a). These results for women's attractiveness suggest that women's facial attractiveness may contain at least two different types of health information; information that is indexed by cortisol and information that is indexed by adiposity. However, that another recent study (Gonzalez-Santoyo et al., 2015) observed no significant correlation between women's cortisol and ratings of their facial attractiveness suggests that the association between attractiveness and cortisol reported by Rantala et al. (2013a)

may not be robust. Consequently, the current study attempted to replicate Rantala et al's (2013a) results for cortisol, adiposity, and women's facial attractiveness.

2.2 Methods

Ninety-six white women (mean age=21.42 years, SD=3.02 years) at University of Glasgow (UK) came into the lab once a week for five weeks (i.e., each participant completed five test sessions in total). Participants were recruited to the study only if they were not currently using any hormonal supplements (e.g., oral contraceptives) and had not used any form of hormonal supplements in the 90 days prior to their participation. None of the participants reported being pregnant, having been pregnant recently, or breastfeeding. All aspects of the study had been approved by our local ethics committee and all participants provided written consent prior to participating.

In each of the five test sessions, each woman first cleaned her face with hypoallergenic face wipes to remove any make up. A full-face digital photograph was taken a minimum of 10 minutes later. Photographs were taken against a constant background, under standardized lighting conditions, and participants were instructed to pose with a neutral expression and looking directly at the camera. 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 other recent studies (e.g., Jones et al., 2015), face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001). Images were aligned on pupil position and masked so that hairstyle and clothing were not visible. Only the face photograph from each participant's first test session was used in the current study.

In each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, smoking,

drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Each individual woman's test sessions took place at approximately the same time of day. Twenty-nine of the women were tested between 10am and 11am each time, 14 of the women were tested between 12pm and 1pm each time, 13 of the women were tested between 1pm and 2pm each time, 14 of the women were tested between 2pm and 3pm each time, and 15 of the women were tested between 3pm and 4pm each time. Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary Cortisol Enzyme Immunoassay Kit 1-3002. All assays passed Salimetrics' quality control. The average cortisol level for each participant was calculated for use in analyses by averaging cortisol values for each woman from all five of her test sessions ($M=0.23\ \mu\text{g/dL}$, $SD=0.12\ \mu\text{g/dL}$).

Each participant's height ($M=166.22\ \text{cm}$, $SD=5.30\ \text{cm}$) and weight ($M=65.23\ \text{kg}$, $SD=12.61\ \text{kg}$) was measured and used to calculate their BMI ($M=23.53\ \text{kg/m}^2$, $SD=3.92\ \text{kg/m}^2$). According to the World Health Organization's (WHO) classifications (WHO, 2000), 5 of the women were in the underweight BMI category ($<18.5\ \text{kg/m}^2$), 65 of the women were in the normal category ($18.5\text{--}24.99\ \text{kg/m}^2$), 19 of the women were in the overweight category ($25\text{--}29.99\ \text{kg/m}^2$) and 7 of the women were in the obese category ($>30\ \text{kg/m}^2$).

207 men and 266 women (mean age= 24.14 years, $SD=6.03$ years) rated the faces for attractiveness, health, femininity, or weight in an online study using 1 (low) to 7 (high) scales. Each participant rated the faces on only one of these dimensions and the dimension that any participant was allocated to rate the faces on was randomly determined. Each participant also rated only a randomly selected subset of 40 of the 96 faces. Trial order was fully randomized. Using the same paradigm, a different group of 52 men and 67 women (mean age= 24.97 years, $SD=10.89$ years) rated the faces for dominance. Of the participants in the face rating part of the study, 73% reported they were White, 5% reported they were East Asian, 4% reported they were West Asian, and 2% reported they were Black. The remaining

participants either reported their ethnicity as “other” or chose not to report their ethnicity.

Inter-rater reliability for all 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 each dimension. The average correlation was high for each of the five dimensions (all $r > .87$, all $SD < .02$). 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, health, femininity, dominance, and weight rating for each face. These average ratings were used in our analyses.

2.3 Results

To control for possible effects of diurnal shifts in hormone levels (Papacosta & Nassis, 2011), average cortisol values were standardized for time of day prior to analyses. This was done by grouping participants by hour of testing (between 10am and 11am, between 12pm and 1pm, between 1pm and 2pm, between 2pm and 3pm, or between 3pm and 4pm) and converting average cortisol values within each group to z-scores. Women’s cortisol levels from the first test session (i.e., the test session in which the photograph presented in the face rating part of the study had been taken) were also standardized in this way. This method for controlling for possible effects of diurnal shifts in cortisol is similar to that used in other studies, in which salivary cortisol levels were standardized for time since waking via conversion to z-scores (e.g., Flinn, 2009).

Table 2.1 shows the simple (i.e., zero-order) correlations among all variables. BMI was negatively and significantly correlated with facial attractiveness ($r = -.43$, $N = 96$, $p < .001$), facial health ($r = -.41$, $N = 96$, $p < .001$), and facial femininity ($r = -.32$, $N = 96$, $p = .002$). BMI was positively and significantly correlated with facial adiposity ($r = .67$, $N = 96$, $p < .001$). BMI was not significantly related to facial dominance ($r = -.09$, $N = 96$, $p = .39$). No significant correlations were observed between average cortisol (all $|r| < .16$, all $N = 96$, all $p > .14$) or first test session cortisol (all $|r| < .15$, all $N = 96$, all

p>.17) and any of the face ratings. Figures showing the relationships between face ratings and BMI (Figure 2.1), average cortisol (Figure 2.2), and first test session cortisol (Figure 2.3) are given in below.

Table 2. 1 r-values (and 2-tailed p values) for linear relationships among all variables. (These were included at the request of a referee)

	Average cortisol	First session cortisol	Attractiveness	Health	Femininity	Adiposity	Dominance	Age
BMI	-.03 (.76)	-.09 (.38)	-.43 (<.001)	-.41 (<.001)	-.32 (.002)	.67 (<.001)	-.09 (.39)	.09 (.38)
Average cortisol		.67 (<.001)	-.11 (.28)	-.10 (.34)	-.08 (.43)	.05 (.60)	.15 (.15)	.18 (.08)
First session cortisol			.09 (.40)	.07 (.48)	.09 (.37)	-.09 (.36)	.14 (.17)	.16 (.13)
Attractiveness				.85 (<.001)	.89 (<.001)	-.59 (<.001)	.26 (.010)	-.07 (.49)
Health					.76 (<.001)	-.52 (<.001)	.17 (.11)	-.10 (.33)
Femininity						-.44 (<.001)	.20 (.053)	-.12 (.23)
Adiposity							-.08 (.43)	-.05 (.63)
Dominance								.24 (.02)

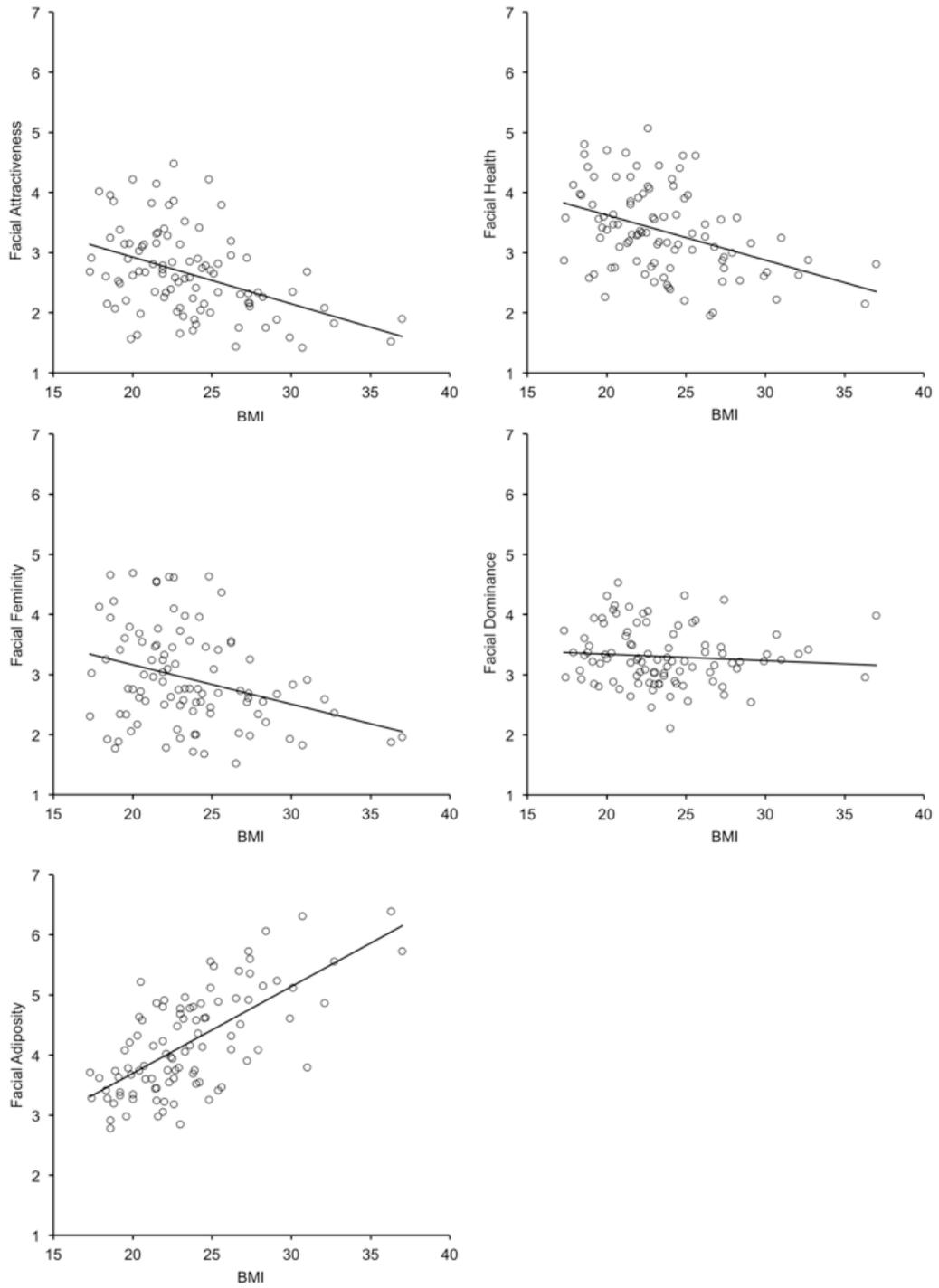


Figure 2. 1 Scatterplots showing relationships between women's BMI and each facial dimension.

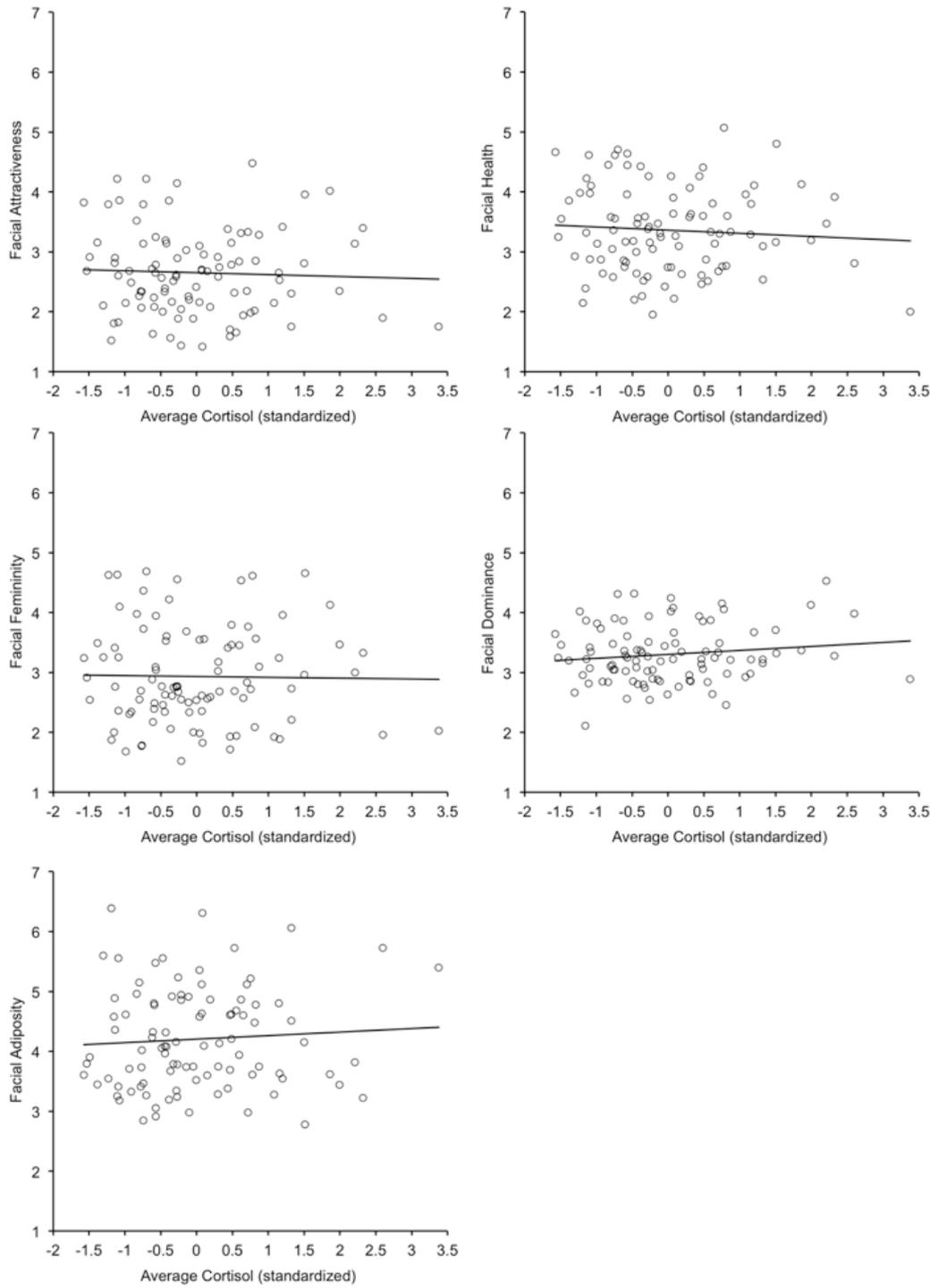


Figure 2. 2 Scatterplots showing relationships between women's average cortisol (standardized for time of day) and each facial dimension.

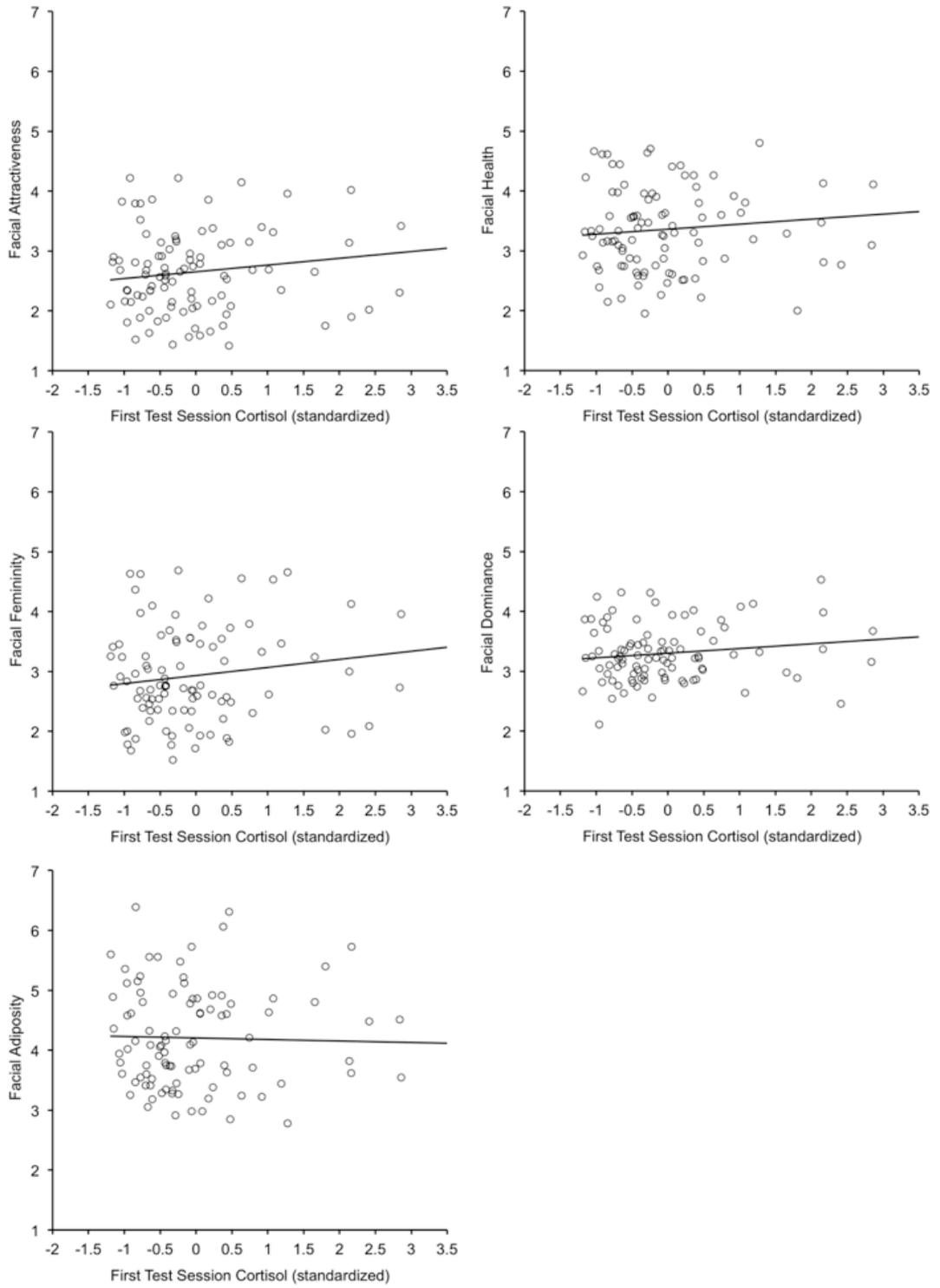


Figure 2. 3 Scatterplots showing relationships between cortisol from first test session (standardized for time of day) and each facial dimension.

Repeating all of the analyses described above with average face ratings derived from either heterosexual male raters' responses only or heterosexual female raters' responses only showed the same pattern of results in all cases (i.e., showed significant relationships between face ratings and BMI, but not between face ratings and either of the cortisol measures). These patterns of results were also seen when non-parametric correlational tests (Spearman's rho) were used.

Finally, we tested whether the relationships between BMI and facial appearance were best characterized by linear or quadratic relationships using the same method reported in Rantala et al. (2013a). BMI was first centered on its mean. A regression analysis in which face ratings were the dependent variable and the centered BMI and the square of the centered BMI were simultaneously entered as predictors was then carried out separately for each of the five facial dimensions considered in our study (facial attractiveness, health, femininity, dominance, and adiposity). For attractiveness ratings, this analysis showed a significant negative linear relationship between BMI and attractiveness ($t=-3.60$, standardized beta $=-.41$, $p=.001$). The quadratic relationship was not significant ($t=-0.31$, standardized beta $=-.04$, $p=.76$). Similar patterns of results were observed for the analyses of health (linear: $t=-3.55$, standardized beta $=-.41$, $p=.001$; quadratic: $t=-0.03$, standardized beta $=-.003$, $p=.98$) and femininity (linear: $t=-2.24$, standardized beta $=-.27$, $p=.027$; quadratic: $t=-0.73$, standardized beta $=-.09$, $p=.47$) ratings. The analysis of adiposity ratings showed a significant positive linear relationship between BMI and adiposity ratings ($t=7.48$, standardized beta $=.70$, $p<.001$). The quadratic relationship was not significant ($t=-0.45$, standardized beta $=-.04$, $p=.65$). For dominance ratings, neither the linear ($t=-1.66$, standardized beta $=-.21$, $p=.10$) nor quadratic relationships were significant ($t=-1.66$, standardized beta $=-.21$, $p=.10$).

2.4 Discussion

Consistent with other recent studies (e.g., Coetzee et al., 2009; Tinlin et al., 2014), we found that ratings of women's facial adiposity were strongly correlated with their actual BMI. These results indicate the existence of facial cues of BMI in women's

faces (see also Windhager et al., 2013 for corresponding evidence from studies of percentage body fat, rather than BMI). We also found that women with lower BMIs tended to have more attractive, healthier-looking faces. A similar relationship was observed for femininity ratings of women's faces (i.e., women with lower BMIs were rated as looking more feminine), which is a novel result not previously reported in the literature. These results suggest that cues of adiposity are important for social judgments of women's faces.

We observed no significant correlations between ratings of women's faces and their cortisol levels. This pattern was seen both when average cortisol levels (i.e., cortisol levels collapsed across test sessions) were analyzed and when only cortisol levels from the same test session as the photograph were analyzed. These null results contrast with Rantala et al. (2013a), who recently reported a significant negative relationship between women's facial attractiveness and cortisol. Like our study, Gonzalez-Santoyo et al. (2015) also reported no significant correlations between women's cortisol and facial attractiveness and femininity. However, and unlike our study, Gonzalez-Santoyo et al. (2015) observed a significant negative correlation between cortisol and women's facial dominance.

There are several possible explanations for these inconsistent results. For example, effects of changes in women's facial appearance over the menstrual cycle (e.g., Puts et al., 2013), which were controlled for only in Rantala et al. (2013a), may have obscured relationships between attractiveness and cortisol in the current study and Gonzalez-Santoyo et al's (2015) study. It is also possible that the inconsistent results reflect cross-cultural differences in social judgments of faces and/or the nature of the relationships between hormones and appearance, since the studies were conducted using different populations. Differences in the visibility of hairstyle, hair-quality, and clothing across studies, whether plasma or salivary cortisol levels were investigated, and differences in how researchers controlled for possible effects of diurnal shifts in cortisol levels may also have contributed to the inconsistencies. Future research exploring these, and other, possibilities may help clarify the reasons for the inconsistent results across studies.

Some previous research on the relationship between women's facial appearance and measures of their adiposity reported that overweight and underweight women were more attractive and healthier-looking than women with normal adiposity levels and that these quadratic relationships explained variation in facial appearance better than simple linear relationships did (e.g., Coetzee et al., 2009; Rantala et al., 2013). By contrast with these results, here we found that linear relationships between BMI and facial appearance explained more of the variation in attractiveness, health, and femininity than did the corresponding quadratic relationships. Importantly, we emphasize here that these results do not indicate that very thin women have particularly attractive, healthy, or feminine faces; according to the World Health Organization's classifications (WHO, 2000) only 5 of the 96 women in our study were underweight.

Our results linking perceptions of women's facial attractiveness, health and femininity to their BMI present further evidence for the existence of health cues in women's faces and the importance of adiposity cues for social judgments of women's faces. That no relationships were observed between ratings of women's faces and cortisol suggests that the associations reported in two recent studies might not necessarily be robust (Gonzalez-Santoyo et al., 2015; Rantala et al., 2013a). Our results for perceptions of women's facial attractiveness, health, and femininity then raise the possibility that the types of health information reflected in women's faces include qualities that are indexed by BMI, but do not necessarily include qualities that are indexed by cortisol. That facial adiposity appears to be a particularly important health cue for judgments of *women's* attractiveness is consistent with other recent work suggesting that facial adiposity is a particularly important health cue for judgments of *men's* attractiveness (Rantala et al., 2013b).

The work reported in Chapter 2 presents further evidence for visible adiposity cues in women's faces. However, it also casts doubt over the recent claims that women's facial attractiveness and dominance is correlated with the stress hormone cortisol (Gonzalez-Santoyo et al., 2015; Rantala et al., 2013a). While this chapter

focused on links between physical measures and women's faces, Chapter 3 will examine hypothesized links between physical characteristics thought to index men's threat potential and aspects of their facial appearance.

Chapter 3

Interrelationships among men's threat potential, facial dominance, and vocal dominance

The following chapter is based on work published in *Evolutionary Psychology*.

Han, C., Kandrik, M., Hahn, A. C., Fisher, C. I., Feinberg, D. R., Holzleitner, I. J., DeBruine, L. M., & Jones, B. C. (2017). Interrelationships Among Men's Threat Potential, Facial Dominance, and Vocal Dominance. *Evolutionary Psychology*, 15(1), 1474704917697332.

Abstract

The benefits of minimizing the costs of engaging in violent conflict are thought to have shaped adaptations for the rapid assessment of others' capacity to inflict physical harm. Although studies have suggested that men's faces and voices both contain information about their threat potential, one recent study suggested that men's faces are a more valid cue of their threat potential than their voices are. Consequently, the current study investigated the interrelationships among a composite measure of men's actual threat potential (derived from measures of their upper-body strength, height, and weight) and composite measures of these men's perceived facial and vocal threat potential (derived from dominance, strength, and weight ratings of their faces and voices, respectively). Although men's perceived facial and vocal threat potential were positively correlated, men's actual threat potential was related to their perceived facial, but not vocal, threat potential. These results present new evidence that men's faces may be a more valid cue of these aspects of threat potential than their voices are.

3.1 Introduction

Evidence suggests that aggressive conflict among ancestral males has been an important selection pressure (Manson & Wrangham, 1991; Keeley, 1996) that may have led to adaptations for assessing the threat potential of others prior to actual combat (Puts, 2010; Sell et al., 2009). Much of the research into cues of threat potential in humans has investigated the relationships between measures of men's threat potential (e.g., measures of their upper-body strength, height, or weight) and their facial or vocal characteristics (reviewed in Puts, 2010; Puts, Jones, & DeBruine 2012).

Several studies have reported positive correlations between measures of men's upper-body strength (e.g., their handgrip strength) and ratings of their faces for dominance or strength (Fink et al., 2007; Holzleitner & Perrett, 2016; Sell et al., 2009; Windhager et al., 2011). Strength ratings of men's voices are also positively correlated with measures of their actual physical strength (Sell et al., 2010) and men's voices have been shown to contain acoustic characteristics that are correlated with their strength, height, and/or weight (Hill et al., 2013; Hodges-Simeon et al., 2014; Puts et al., 2012; Pisanski et al., 2016). Other work has found that taller men's faces are perceived to be more dominant (Burton & Rule, 2013; Re et al., 2013). People can also predict the winners of mixed martial arts fights from facial cues alone at levels greater than chance (Little et al., 2015). Collectively, these results suggest that both faces and voices contain cues of men's threat potential. However, research reporting that men's fighting ability can be assessed from their faces, but not their voices, suggests that faces may be a more valid cue of some aspects of men's threat potential than their voices are (Doll et al., 2014).

In light of Doll et al's (2014) recent findings for fighting ability, we investigated the relationships among men's actual threat potential and ratings of both their perceived facial and vocal threat potential. Men's actual threat potential was assessed via a composite measure derived from a principal component analysis of their handgrip strength, height, and weight. Perceived facial and vocal threat

potential were assessed via composite measures derived from principal component analyses of dominance ratings, strength ratings, and weight ratings of their faces and voices, respectively. Men's handgrip strength, face photographs, and voice recordings were collected on five separate occasions to ensure we obtained representative measures of men's strength, facial appearance, and vocal appearance. Given Doll et al's (2014) findings, we predicted that the composite measure of men's threat potential would be more strongly correlated with the composite measure of their perceived facial threat potential than with the composite measure of their perceived vocal threat potential.

3.2 Methods

Forty-four men (mean age=22.02 years, SD=3.41 years) each completed five weekly test sessions as part of a larger study on possible relationships among hormone levels and voice perceptions (Kandrik et al., 2016). In each of the five test sessions, each participant first cleaned his face with hypoallergenic face wipes. A full-face digital photograph was taken a minimum of 10 minutes later. Photographs were taken in a small windowless room against a constant background, under standardized diffuse lighting conditions, and 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 other recent work on social judgments of faces (e.g., Jones et al., 2015), face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001). Images were masked so that hairstyle and clothing were not visible and standardized in size and orientation on pupil positions.

In each of the five test sessions, a digital voice recording of each man was taken in mono using an Audio-Technica AT-4041 cardioid condenser microphone at a sampling rate of 44.1 kHz at 16-bit amplitude quantization. Each man was

instructed to say “Hi, I’m a student at the University of Glasgow” in their normal speaking voice. The word “hi” was then extracted from each recording for use in the rating part of the study. The sound pressure level of all voices was amplitude normalized to 70 decibels using the root mean squared method.

In each of the five test sessions, each man’s handgrip strength was measured four times using a T. K. K. 5001 Grip A dynamometer, alternating between the dominant (M=42.15 kgf, SD=7.84 kgf) and non-dominant (M=40.02 kgf, SD=6.83 kgf) hand. Two men were left-handed and 42 were right-handed. In addition, each man’s height (M=178.5 cm, SD=6.75 cm) and weight (M=72.65 kg, SD=9.43kg) was measured in one of the test sessions. Height, weight, and handgrip strength have been previously used to assess men’s threat potential (e.g., Puts et al., 2012).

Next, the face photographs of the 44 men (220 face photographs in total) and the voice recordings of the 44 men (220 voice recordings in total) were rated for dominance, strength, and weight using 1 (low) to 7 (high) scales. Faces and voices were presented in separate blocks of trials, and dominance, strength, and weight were rated in separate blocks of trials, respectively. Trial order was fully randomized within each block. None of the traits were defined for the raters and height was not rated. Thirty-two men and 47 women (mean age=23.28 years, SD=4.34 years) rated the faces and voices. The number of traits that each rater rated varied across raters. Each individual rater was randomly allocated to rate between 2 and 4 blocks of trials (mean number of raters per block of trials=31.83, SD=3.13). One rater chose not to report their age. Inter-rater agreement was high for all combinations of trait and stimulus type (all Cronbach’s alphas>.89).

Consequently, we calculated the mean dominance (face: M=3.60, SD=0.74; voice: M=3.86, SD=0.67), strength (face: M=3.93, SD=0.81; voice: M=3.86, SD=0.72), and weight (face: M=4.26, SD=0.83; voice: M=4.01, SD=0.59) rating for each man’s face and voice. Separate analyses of men’s and women’s ratings showed the same pattern of significant results as analyses of these combined ratings. Intercorrelations among ratings for each combination of trait and stimulus type across test sessions are given in Table 3.1.

Table 3. 1 Inter-correlations among test sessions for each trait.

Trait	Mean <i>r</i> value	SD
Vocal weight	0.80	0.60
Vocal strength	0.84	0.78
Vocal dominance	0.78	0.74
Facial weight	0.78	0.87
Facial strength	0.96	0.84
Facial dominance	0.90	0.78

3.3 Results

First, we subjected ratings of men's faces to principal component analysis with no rotation. This analysis produced a single component that explained approximately 75% of the variance in scores and was highly correlated with facial strength ($r=.98$), dominance ($r=.91$), and weight ($r=.67$) ratings. We labeled this component the *perceived facial threat potential component*.

Next, we subjected ratings of men's voices to principal component analysis with no rotation. This analysis produced a single component that explained approximately 82% of the variance in scores and was highly correlated with strength ($r=.98$), dominance ($r=.88$), and weight ($r=.85$) ratings. We labeled this component the *perceived vocal threat potential component*.

We also subjected our four measures of men's threat potential (handgrip strength for dominant hand, handgrip strength for non-dominant hand, height, and weight) to principal component analysis with no rotation. This analysis produced a single component that explained approximately 60% of the variance in scores and was highly correlated with handgrip strength for non-dominant hand ($r=.93$), handgrip strength for dominant hand ($r=.89$), weight ($r=.68$), and height ($r=.54$). We labeled this component the *actual threat potential component*.

Scores on the *perceived facial threat potential component* were positively correlated with scores on both the *perceived vocal threat potential component* ($r=.37$, $N=44$, $p=.012$) and the *actual threat potential component* ($r=.32$, $N=44$, $p=.033$). Scores on the *perceived vocal threat potential component* and the *actual threat potential component* were not significantly correlated ($r=-.02$, $N=44$, $p=.92$). Steiger's test (Steiger, 1980) showed that the correlation between the *actual threat potential component* and the *perceived facial threat potential component* was significantly stronger than the correlation between the *actual threat potential component* and the *perceived vocal threat potential component* ($z=1.97$, $p=.049$). Table 3.2 shows intercorrelations among all variables.

Table 3. 2 Inter-correlations among all individual variables.

	Facial dominance rating	Facial strength rating	Facial weight rating	Vocal dominance rating	Vocal strength rating	Vocal weight rating	Height	Weight	Dominant handgrip strength
Facial strength rating	.92 (.001)								
Facial weight rating	.32 (.037)	.54 (.001)							
Vocal dominance rating	.14 (.354)	.22 (.159)	.09 (.555)						
Vocal strength rating	.33 (.028)	.40 (.007)	.18 (.251)	.86 (.001)					
Vocal weight rating	.39 (.009)	.49 (.001)	.34 (.024)	.53 (.001)	.80 (.001)				
Height	-.01 (.935)	.02 (.878)	.01 (.939)	.08 (.602)	.04 (.782)	.07 (.666)			
Weight	.15 (.320)	.32 (.033)	.78 (.001)	.02 (.878)	.04 (.783)	.28 (.063)	.25 (.107)		
Dominant handgrip strength	.20 (.196)	.26 (.090)	.23 (.137)	-.04 (.822)	-.13 (.389)	-.10 (.521)	.25 (.100)	.43 (.004)	
Non-dominant handgrip strength	.20 (.206)	.26 (.086)	.20 (.186)	-.07 (.640)	-.11 (.466)	-.02 (.904)	.38 (.010)	.46 (.002)	.87 (.001)

Note. Table shows r values and 2-tailed p values in parentheses.

3.4 Discussion

Principal component analysis of men's handgrip strength, weight, and height produced a single "actual threat potential" component. This result is consistent with previous work suggesting that these measures are positively correlated indices of men's threat potential (Puts et al., 2012). Moreover, principal component analyses of the face and voice ratings each revealed a single perceived threat potential component. This result is consistent with previous research suggesting that impressions of men's strength, dominance, and body size are positively intercorrelated (e.g., Holzleitner & Perrett, 2016). Further analyses showed that men's perceived facial threat potential was positively related to their scores on the actual threat potential component. This result is consistent with previous research suggesting that men's faces contain cues to their actual threat potential (Burton & Rule, 2013; Doll et al., 2014; Fink et al., 2007; Hill et al., 2013; Holzleitner & Perrett, 2016; Re et al., 2013; Sell et al., 2009; Windhager et al., 2011). By contrast with our results for facial dominance, we found no evidence that people could judge men's threat potential from their voices. Our results then complement those of Doll et al. (2014), who found that men's fighting ability could be better assessed from their faces than their voices. While Doll et al. (2014) observed this pattern of results when men's threat potential was measured from acquaintances' ratings of their fighting ability, here we see the same pattern of results for analyses of anthropometric measures of men's threat potential. While some other studies with larger sample sizes have reported significant correlations between perceptions of men's voices and measures of their threat potential (e.g., Sell et al., 2010), both our results and those of Doll et al. (2014) suggest that men's faces are more valid cues to their threat potential than their voices are. Because Doll et al. (2014) used full sentences as their voice stimuli, the pattern of results that we observed in the current study is unlikely to be a consequence of the short snippets of speech we used as stimuli.

One recent study found that ratings of men's facial and vocal dominance were negatively correlated (Rezlescu et al., 2015). By contrast with Rezlescu et al's (2015) results, the current study found that men's scores on the perceived facial and vocal threat potential components were positively and significantly correlated.

In other words, our study found that men whose faces looked particularly dominant possessed voices that sounded particularly dominant. The positive correlation between facial and vocal threat potential observed in the current study is consistent with other research reporting correlations between perceptions of faces and voices (reviewed in Smith et al., 2016) and suggests that men's faces and voices contain some overlapping information about their perceived threat potential. Our results suggest that the overlapping information in the perceived dominance of men's faces and voices is unlikely to include information about their upper-body strength, height, or weight. It is possible that this correlation is driven by cues of men's aggressiveness or emotional state (e.g., anger), rather than threat potential, per se.

In our study, participants rated the faces and voices for dominance, strength, and weight. It is possible that weight ratings of faces and voices are shaped by cues of adiposity, rather than formidability, per se. However, the results of our PCAs show that there is substantial overlap between weight, strength, and dominance ratings of men's faces (see also voices). Thus, whatever information participants do use when they rate faces or voices for weight does seem to be highly correlated with the information that they use when making more direct assessments of formidability (strength and dominance ratings). A further unresolved question is what specific facial characteristics are valid cues of men's threat potential. To date, most research addressing this question has focused on facial measurements of putative sexually dimorphic aspects of facial morphology. Such measures may be error prone in 2D images, however, due to difficulties controlling for head tilt, among other factors (e.g., Schneider et al., 2012).

In summary, we found that a composite measure of men's actual threat potential (derived from measures of their upper-body strength, height, and weight) was positively correlated with a composite measure of these men's perceived facial, but not vocal, threat potential (derived from dominance, strength, and weight ratings of their faces and voices, respectively). Together with Doll et al's (2014) results for men's fighting ability, these findings suggest that men's faces may be a more valid cue to some aspects of their threat potential than their voices are.

Chapters 2 and 3 demonstrated correlations between measures of body size and aspects of women's (Chapter 2) and men's (Chapter 3) facial appearance. The links observed are most likely driven by shape information (e.g., facial shape cues of adiposity). However, several lines of evidence have recently demonstrated that facial color cues may also index health and influence facial attractiveness judgments. Interestingly, these effects are hypothesized to be similar across cultures, although the evidence for this latter claim is weak. Consequently, in Chapter 4, we investigated the effects of manipulating color cues on White UK and Chinese faces on White UK and Chinese participants' judgments of attractiveness and health.

Chapter 4

Cultural differences in preferences for facial coloration

The following chapter is based on work published in *Evolution and Human Behaviour*.

Han, C., Wang, H., Hahn, A. C., Fisher, C. I., Kandrik, M., Fasolt, V., Morrison, D. K., Lee, A. L., Holzleitner, A. J., DeBruine, L. M., & Jones, B. C. (In Press). Cultural differences in preferences for facial coloration. *Evolution and Human Behaviour*.

Abstract

Effects of facial coloration on attractiveness judgments are hypothesized to be “universal” (i.e., similar across cultures). However, only two studies have directly compared facial color preferences in two cultures. Both of those studies reported that White UK and Black African participants showed similar preferences for facial coloration. By contrast with the cross-cultural similarity reported in those studies, here we show cultural differences in the effects of facial coloration on Chinese and White UK participants' (N=196) facial attractiveness judgments. While both Chinese and White UK participants preferred faces with increased lightness and redness, Chinese participants had stronger preferences for lightness and White UK participants had stronger preferences for redness. More strikingly, while Chinese participants preferred faces with decreased yellowness, White UK participants preferred faces with increased yellowness, and this effect was not qualified by face ethnicity. These results suggest that preferences for facial coloration are not necessarily universal, but can differ across cultures.

4.1 Introduction

Facial attractiveness judgments predict important social outcomes, such as decisions about who we choose to date, mate with, hire, and vote for (Langlois et al., 2000; Little, Jones, & DeBruine, 2011; Rhodes, 2006). Consequently, identifying factors that influence facial attractiveness judgments can provide insight into the mechanisms and processes that underpin a potentially important driver of social behavior and outcomes (Langlois et al., 2000; Little et al., 2011; Rhodes, 2006). Establishing whether facial characteristics have similar effects on attractiveness judgments in different cultures is a first step in investigating this issue (Langlois et al., 2000; Little et al., 2011; Rhodes, 2006). Many researchers have reported “universal” preferences for aspects of face shape (see Little et al., 2011 and Rhodes, 2006 for reviews).

Effects of skin characteristics on facial attractiveness judgments are at least as large as (if not larger than) those of shape characteristics (Stephen et al., 2012; Said & Todorov, 2011; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010; Torrance, Wincenciak, Hahn, DeBruine, & Jones, 2014). Independently increasing yellowness, lightness, or redness in face images increases both their attractiveness and perceived health (Fisher, Hahn, DeBruine, & Jones, 2014; Kandrik et al., 2017; Stephen, Law Smith, Stirrat, & Perrett, 2009a; Stephen, Coetzee, Law Smith, & Perrett, 2009b; Stephen, Coetzee, & Perrett, 2011; see also Lefevre et al., 2013). These preferences are independent of possible effects of facial cues to ethnicity and are hypothesized to reflect adaptations that function to identify individuals in good physical health (Stephen et al., 2011, 2012). However, evidence that facial coloration is associated with measures of good physical health is equivocal (Foo, Rhodes, & Simmons, 2017; Foo, Simmons, & Rhodes, 2017; Henderson et al., 2017; Phalane et al., 2017).

Effects of facial coloration on attractiveness judgments and health perceptions are hypothesized to be universal (Stephen et al., 2011, 2012). However, only two studies have directly compared facial color preferences in two cultures (Coetzee, Greeff, Stephen, & Perrett, 2014; Stephen et al., 2012). Coetzee, Greeff, Stephen,

and Perrett (2014) and Stephen et al. (2012) reported similar correlations between facial coloration and attractiveness in White UK and Black African participants. Studies investigating relationships between facial coloration and attractiveness judgments in either White UK or Black African samples have also reported similar preferences (e.g., Coetzee et al., 2012).

If preferences for facial coloration are similar across cultures then similarity in facial color preferences should be evident in cross-cultural comparisons other than the comparisons of White UK and Black African participants reported by Coetzee, Greeff, Stephen, and Perrett (2014) and Stephen et al. (2012). To investigate this issue, we compared Chinese and White UK participants' attractiveness judgments of faces that had been independently manipulated in global yellowness, lightness, and redness.

4.2 Methods

4.2.1 Participants

In total, 196 participants took part in the study. These included 52 White UK men ($M_{\text{age}} = 22.83$ years, $SD = 5.55$ years) and 49 White UK women ($M_{\text{age}} = 21.82$ years, $SD = 3.64$ years), all of whom were born and resided in the UK. They also included 48 Chinese men ($M_{\text{age}} = 24.47$ years, $SD = 3.64$ years) and 47 Chinese women ($M_{\text{age}} = 24.00$ years, $SD = 2.75$ years), all of whom were born in China, but currently resided in the UK (mean number of years in the UK = 1.06 years, $SD = 0.95$ years).

4.2.2 Stimuli

First, full-face photographs of 5 young adult White UK men, 5 young adult White UK women, 5 young adult Chinese men, and 5 young adult Chinese women were taken under standardized photographic conditions. All individuals photographed were between 18 and 23 years old and were students at the University of Glasgow. Photographs were taken in a small windowless room against a constant background, under standardized diffuse lighting conditions, and participants were instructed to pose with a neutral expression. Camera-to-head distance and camera

settings were held constant. 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. These face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong, Luo, & Rhodes, 2001) and standardized on pupil positions.

CIELab color space (Commission Internationale de L'Éclairage, 1976) is modeled on the human visual system and consists of three independent color axes: yellow (b^*), lightness (L^*), and red (a^*). We independently manipulated global coloration in the face images along each of these axes. Using methods described in Stephen et al. (2009a), we created six versions of each original face: One in which yellow was increased by three units, one in which yellow was decreased by three units, one in which lightness was increased by three units, one in which lightness was decreased by three units, one in which red was increased by three units, and one in which red was decreased by three units. Importantly, these manipulations only affect the manipulated color dimension (e.g., altering redness does not affect yellowness or lightness) 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., Fisher et al., 2014; Kandrik et al., 2017; Stephen et al., 2011; Whitehead et al., 2012). These color manipulations, in which color values were increased or decreased by 3 units, are within the normal range of coloration for White UK (Whitehead et al., 2012) and Malaysian Chinese (Tan et al., 2017) adult faces. We manipulated facial color by +/- 3 units because we have previously shown that this magnitude of manipulation produces preferences for facial coloration in White UK participants that are similar to those reported in other studies using White UK faces (Fisher et al., 2014). This process created sixty pairs of faces, where each pair consisted of a version of an identity in which color values on one color axis had been increased by 3 units and another version of the same identity in which color values on that same color axis had been decreased by 3 units. Images were masked so that hairstyle and clothing were not visible. Example stimuli are shown in Figure 4.1.

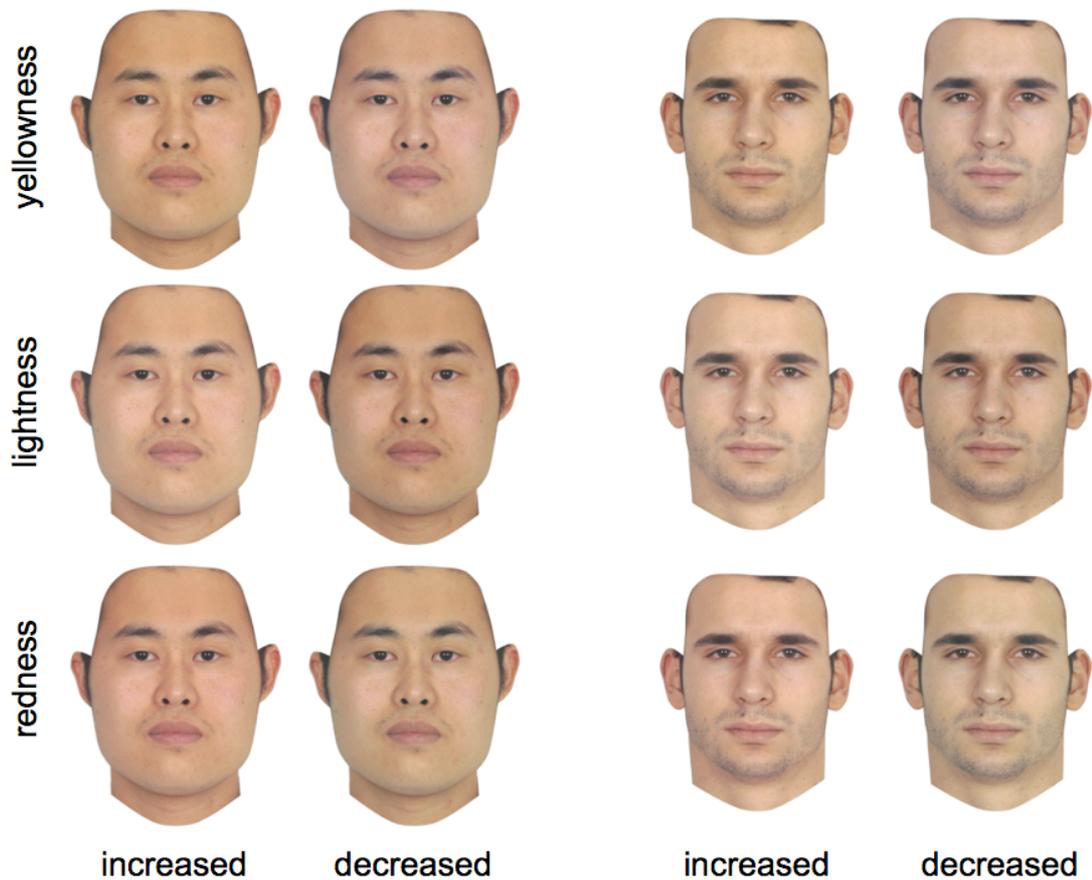


Figure 4. 1 Examples of Chinese and White UK male face stimuli used in our study. The image on the left in each pair has increased color values and the image on the right in each pair has decreased color values. Images were independently manipulated in yellowness (top row), lightness (middle row), and redness (bottom row).

4.2.3 Procedure

The sixty pairs of faces were presented to participants using a two-alternative forced choice paradigm, in which participants were instructed to click on the face that they thought was the more attractive in each pair. In a separate block of trials, participants repeated this task, this time indicating which face in each pair looked healthier, rather than more attractive. These testing procedures control for the effects of prototypicality (i.e., averageness) of facial coloration on attractiveness judgments and health perceptions and have been used in previous work on facial color preferences (e.g., Kandrik et al., 2017). The order of the attractiveness-judgment and health-judgment tasks was fully randomized. Trial order and the side of the screen on which any given image was shown were fully randomized between participants. The screen was calibrated using an xRite i1 Display Pro colorimeter prior to testing.

4.3 Results

Responses on the attractiveness-judgment task were analyzed using mixed binary logistic regression analyses in R v3.3.2 (R Core Team, 2016) with lme4 v1.1-12 (Bates, Maechler, Bolker, & Walker, 2015). Preferences for facial yellowness, lightness, and redness were analyzed in separate models. In each model, the dependent variable was binary choice (0 = *chose version of face with decreased color values*, 1 = *chose version of face with increased color values*). Independent variables were sex of face (male, female), ethnicity of face (White UK, Chinese), sex of participant (male, female), and ethnicity of participant (White UK, Chinese), which were effect coded. For the sex of face and sex of participant variables, -0.5 corresponded to female and +0.5 corresponded to male. For the ethnicity of face and ethnicity of participant variables, -0.5 corresponded to White UK and +0.5 corresponded to Chinese. Each model specified random intercepts for participant and face. Random slopes were specified maximally, following Barr, Levy, Scheepers, and Tily (2013) and Barr (2013). Note that this type of analysis takes into account variation in the effects of the color manipulations across stimuli items (in this study, individual faces, Barr et al., 2013). Formulae and outputs for each model are given in our Supplemental Information, along with analysis scripts. Data are publicly available at osf.io/etxvu/.

4.3.1 Attractiveness judgments and facial yellowness

The effects of facial yellowness on attractiveness judgments are summarized in Figure 4.2. The intercept was significant ($\beta = -0.30$, $z = -2.40$, $p = .017$), indicating that, on average, participants preferred faces with decreased yellowness over those with increased yellowness. This was qualified by a main effect of ethnicity of participant ($\beta = -1.48$, $z = -8.11$, $p < .001$), indicating that Chinese and White UK participants differed significantly in the strength of their preferences for facial yellowness. Follow-up analyses indicated that White UK participants preferred versions of faces with increased yellowness over versions with decreased yellowness (intercept: $\beta = 0.45$, $z = 2.72$, $p = .007$), but Chinese participants preferred versions of faces with decreased yellowness over versions with increased yellowness (intercept: $\beta = -1.01$, $z = -7.05$, $p < .001$).

Our initial analysis also revealed significant main effects of sex of face ($\beta = 0.40$, $z = 2.14$, $p = .032$) and sex of participant ($\beta = 0.44$, $z = 2.42$, $p = .016$). These main effects indicated that preferences for facial yellowness were stronger for judgments of male faces than female faces and stronger for judgments by male participants than female participants. A significant interaction between ethnicity of participant and sex of participant ($\beta = 0.80$, $z = 2.22$, $p = .027$) indicated that the effect of ethnicity of participant on preferences for facial yellowness was larger for female than male participants. No other effects were significant (all absolute β s < 0.51 , all absolute z s < 1.62 , all p s $> .10$).

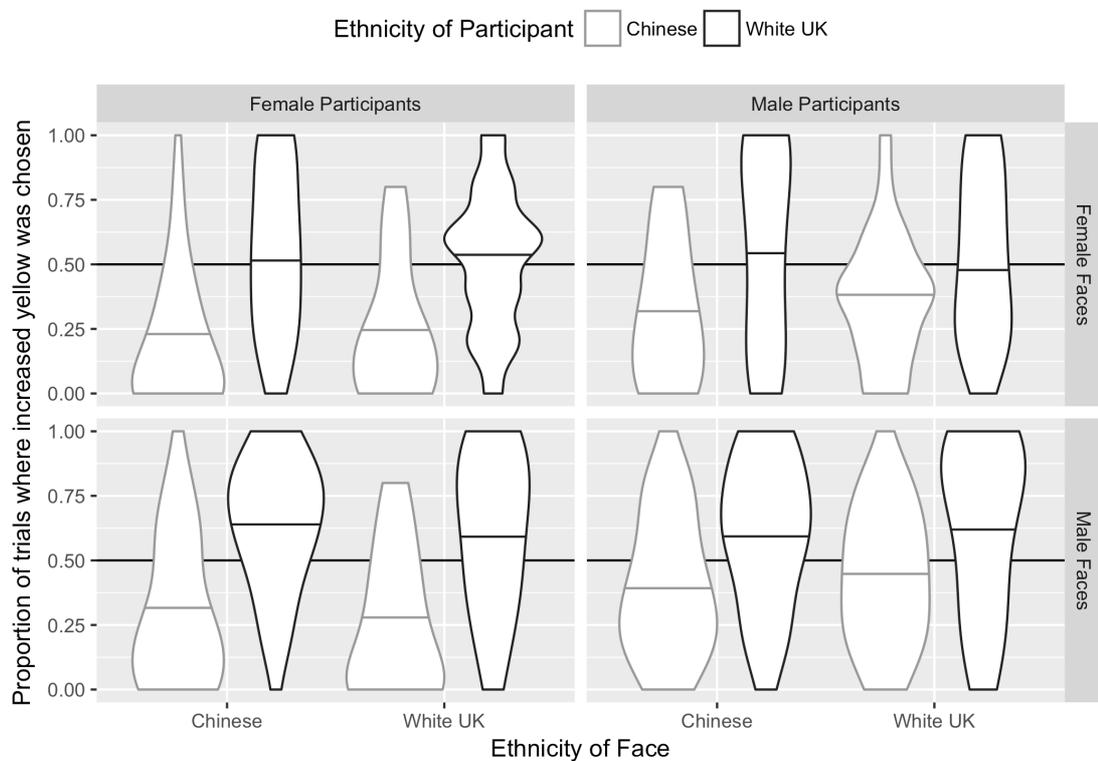


Figure 4. 2 Attractiveness judgments and facial yellowness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in yellowness. The lines indicate medians and 0.5 on the y-axis equals chance.

4.3.2 Attractiveness judgments and facial lightness

The effects of facial lightness on attractiveness judgments are summarized in Figure 4.3. The intercept was significant ($\beta = 1.08$, $z = 10.03$, $p < .001$), indicating that, on average, participants preferred faces with increased lightness

over those with decreased lightness. This was qualified by a main effect of ethnicity of participant ($\beta = 1.53$, $z = 7.55$, $p < .001$), indicating that Chinese participants had stronger preferences for facial lightness than did White UK participants. A significant main effect of sex of face ($\beta = -0.24$, $z = -2.23$, $p = .026$) indicated that preferences for facial lightness were generally stronger for female faces than male faces. A significant interaction between sex of face and ethnicity of participant ($\beta = 0.35$, $z = 2.16$, $p = .031$) indicated that the effect of sex of face on preferences for lightness was larger among White UK than Chinese participants. No other effects were significant (all absolute β s < 0.67 , all absolute z s < 1.63 , all p s $> .05$).

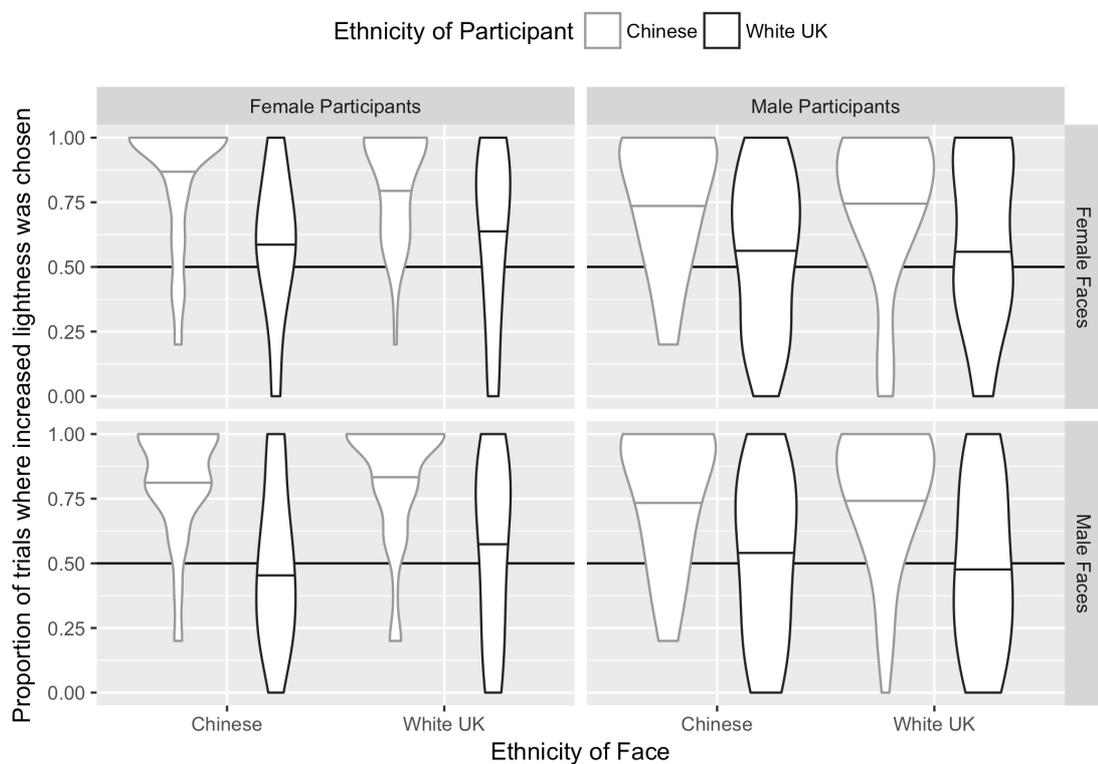


Figure 4. 3 Attractiveness judgments and facial lightness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in lightness. The lines indicate medians and 0.5 on the y-axis equals chance.

4.3.3 Attractiveness judgments and facial redness

The effects of facial redness on attractiveness judgments are summarized in Figure 4.4. The intercept was significant ($\beta = 1.64$, $z = 9.53$, $p < .001$), indicating that, on average, participants preferred faces with increased redness over those with decreased redness. This was qualified by a main effect of ethnicity of participant ($\beta = -0.58$, $z = -2.66$, $p = .007$), indicating that White UK participants had

stronger preferences for redness than did Chinese participants. A significant main effect of sex of face ($\beta = -0.61$, $z = -2.21$, $p = .027$) indicated that preferences for redness were stronger for judgments of female than male faces. There were also significant interactions between sex of face and sex of participant ($\beta = 0.54$, $z = 3.05$, $p = .002$), between ethnicity of face and sex of face ($\beta = -1.14$, $z = -2.04$, $p = .041$), between ethnicity of face and ethnicity of participant ($\beta = -0.35$, $z = -2.02$, $p = .043$). These two-way interactions suggested that the tendency to show stronger preferences for redness in female than male faces was greater in female than male participants, that the tendency to show stronger preferences for redness in female than male faces was greater in Chinese than White UK faces, and that the tendency for White UK participants to show stronger preferences for redness than did Chinese participants was greater for Chinese faces than White UK faces, respectively. The four-way interaction among sex of face, ethnicity of face, sex of participant, and ethnicity of participant was also significant ($\beta = -1.63$, $z = -2.20$, $p = .028$). Figure 4.4 suggested that the four-way interaction reflected the effect of ethnicity of participant being particularly large when male participants judged Chinese male faces. No other effects were significant (all absolute β s < 0.25 , all absolute z s < 1.14 , all p s $> .25$).

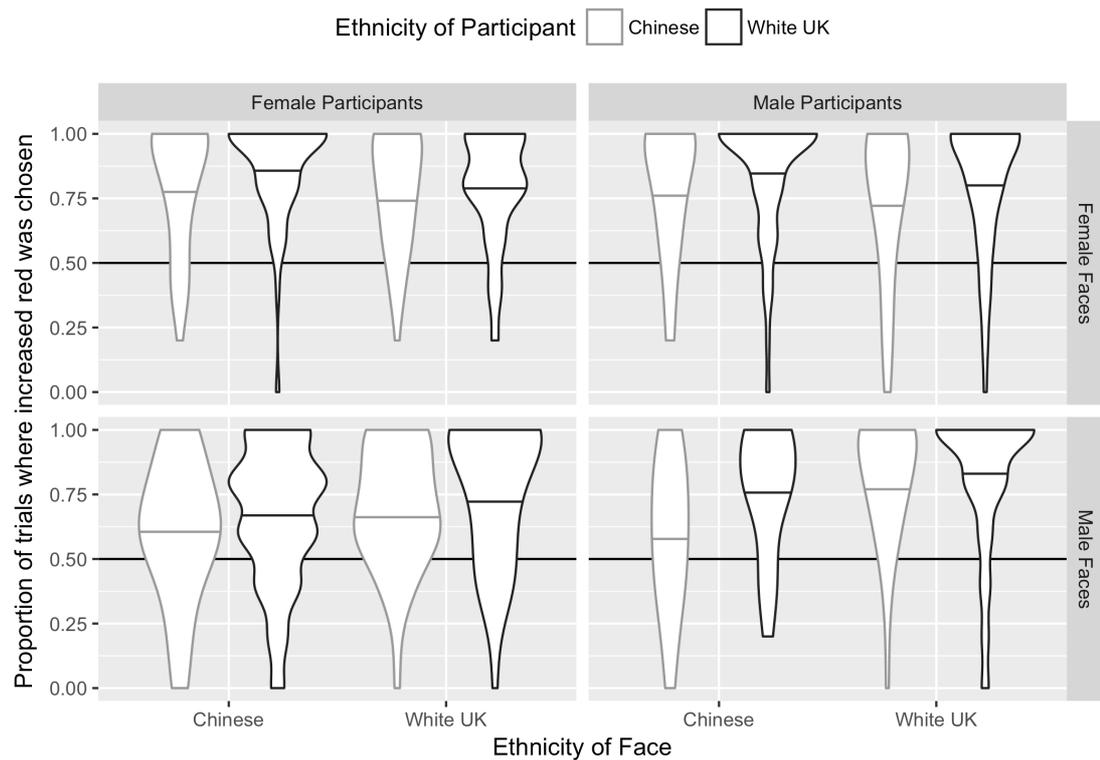


Figure 4. 4 Attractiveness judgments and facial redness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in redness. The lines indicate medians and 0.5 on the y-axis equals chance.

4.3.4 Effects of facial coloration on health perceptions

Responses on the health-judgment task (0=chose version of face with decreased color values, 1=chose version of face with increased color values) were analyzed using mixed binary logistic regression analyses that were identical to those used to analyze responses on the attractiveness-judgment task. Results (given below) were similar to those seen for attractiveness judgments, although the effect of ethnicity of participant was not significant for health judgments of faces manipulated in redness ($p=.08$). An additional Chinese male participant who elected not to do the attractiveness-judgment task did the health-judgment task.

This similarity between our results for attractiveness and health judgments is consistent with previous research suggesting that facial attractiveness and health judgments are generally highly correlated (e.g., Jones et al., 2005). The following figures (figure 4.5, figure 4.6 & figure 4.7) summarize responses for each analysis.

Repeating the analyses described above controlling for possible effects of participant age did not alter the pattern of significant effects.

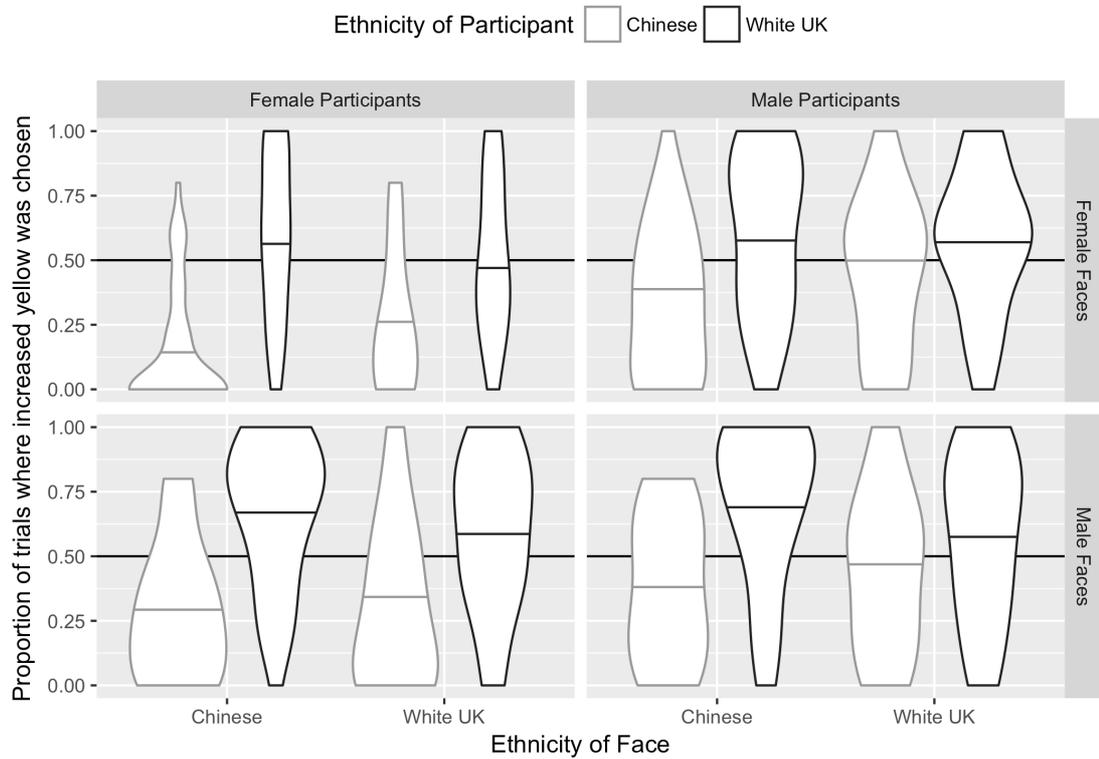


Figure 4. 5 Health Judgments and facial yellowness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in yellowness. The lines indicate medians and 0.5 on the y-axis equals chance.

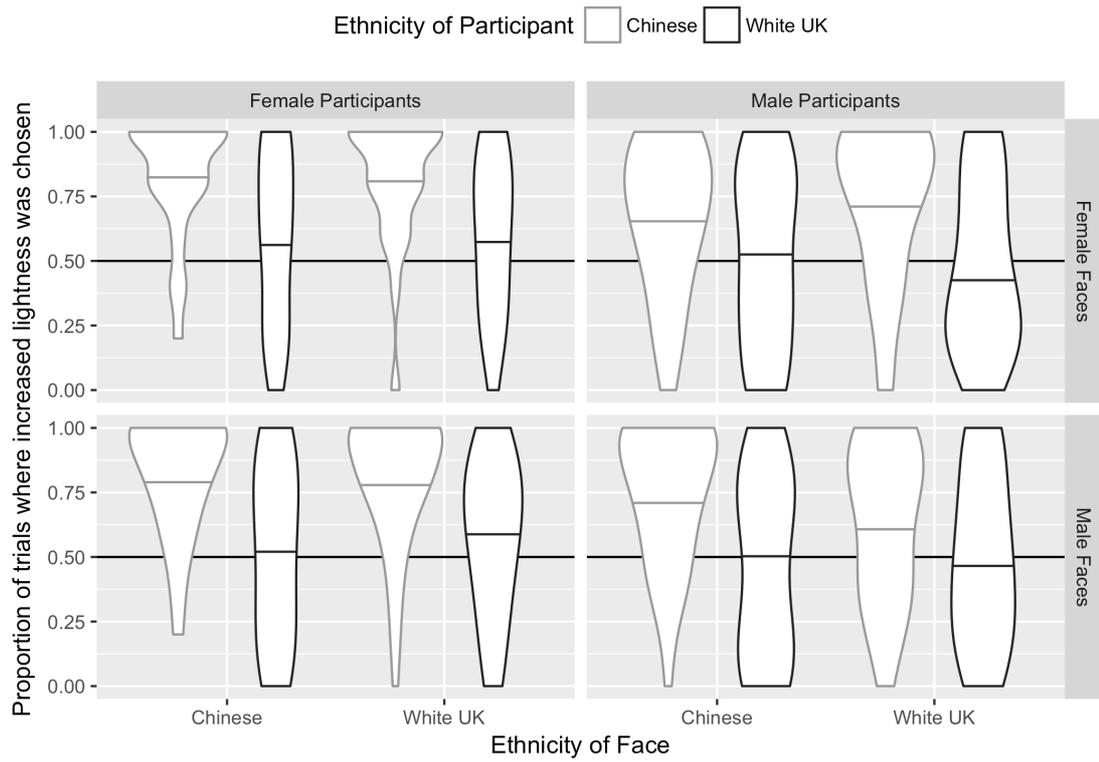


Figure 4. 6 Health judgments and facial lightness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in lightness. The lines indicate medians and 0.5 on the y-axis equals chance.

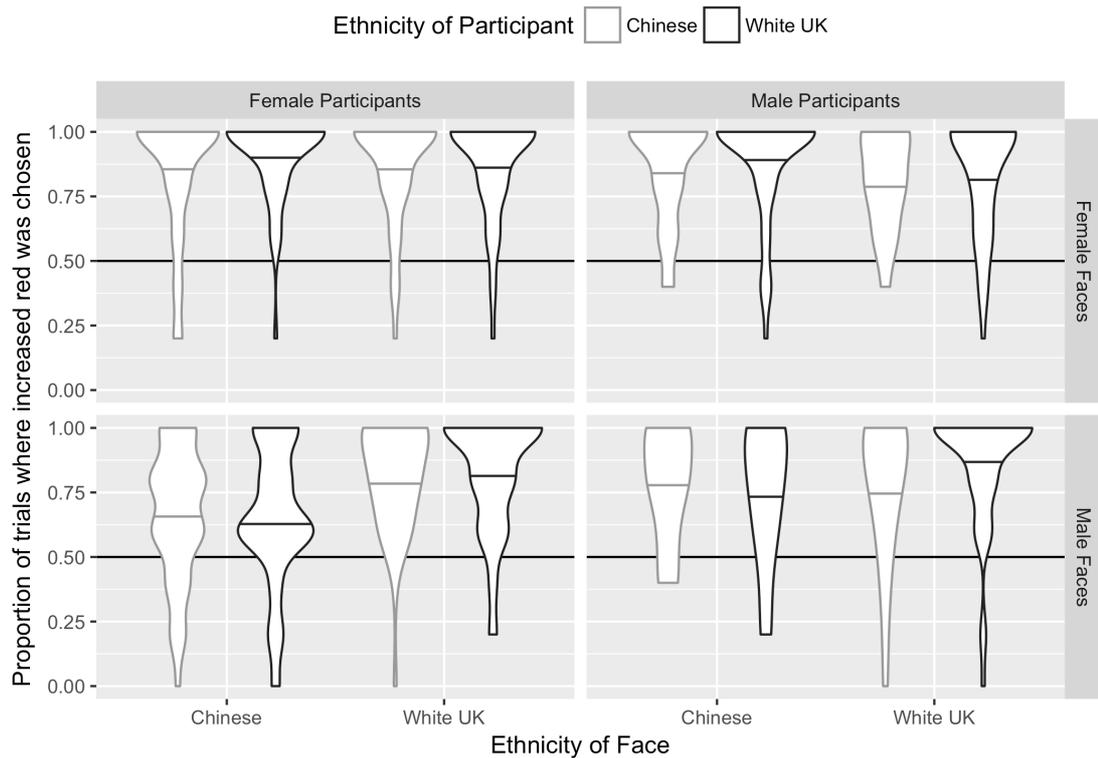


Figure 4. 7 Health judgments and facial redness. Violin plots showing the distribution of Chinese and White UK male and female participants' responses for Chinese and White UK male and female faces manipulated in redness. The lines indicate medians and 0.5 on the y-axis equals chance.

4.4 Discussion

We compared Chinese and White UK participants' attractiveness judgments of faces that had been independently manipulated in global coloration. We show, for the first time, that Chinese participants preferred faces with decreased yellowness to faces with increased yellowness. By contrast, White UK participants preferred faces with increased yellowness to faces with decreased yellowness. These opposite preferences for facial yellowness in Chinese and White UK participants show that preferences for facial coloration are not necessarily universal, as some researchers have suggested (Stephen et al., 2011, 2012), but can differ between cultures.

Our analyses also revealed cross-cultural differences in preferences for facial redness and lightness. Both Chinese and White UK participants preferred faces with increased redness and lightness over those with decreased redness and lightness. However, Chinese participants' preferences for facial redness were

weaker than those observed for White UK participants and Chinese participants' preferences for facial lightness were stronger than those observed for White UK participants.

While our study is the first to compare facial color preferences in Chinese and White UK participants, studies have previously examined facial color preferences in White UK participants. Consistent with their results, the White participants in our study showed preferences for increased facial yellowness, redness, and lightness (Fisher et al., 2014; Kandrik et al., 2017; Stephen et al., 2009a, 2009b, 2011). The stronger preferences for facial lightness when judging female faces than when judging male faces observed in the current study have also been reported previously (Stephen et al., 2009a).

The effects of participant ethnicity on preferences for facial yellowness and lightness in our study were similar for judgments of both own-race and other-race faces. This is an important point, since it demonstrates that the differences in these facial color preferences between Chinese and White UK participants that we observed cannot be explained by hypothesized effects of stimulus ethnicity on preferences for facial coloration (Tan et al., 2017). By contrast, stronger preferences for increased color values in female than male faces could simply be a consequence of sex differences in facial coloration prior to manipulation.

We also observed cross-cultural differences in the effects of facial coloration on health perceptions. In particular, facial yellowness had opposite effects on Chinese and White UK participants' health perceptions. This cross-cultural difference in the effects of yellowness on health perceptions is consistent with recent results suggesting that facial yellowness is not related to actual health. Fruit and vegetable consumption increases facial yellowness in both White UK and Malaysian Chinese participants (e.g., Foo, Rhodes, & Simmons, 2017; Tan, Graf, Mitra, & Stephen, 2017; Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012). While fruit and vegetable consumption is associated with high socioeconomic status in most developed countries, vegetable consumption is associated with low socioeconomic status in

China (Wang, 2001). Consequently, we speculate that aversions to facial yellowness in Chinese participants could be due to facial yellowness functioning as a cue of low status. Alternatively, the cross-cultural differences in preferences for facial yellowness observed in the current study could reflect culture-specific associations between aspects of health and facial coloration, culture-specific stereotypes associated with subtle variation in ethnicity cues, or between-group differences in factors such as socioeconomic status. Further work is needed to investigate these issues.

In conclusion, our analyses of Chinese and White UK participants' preferences for facial coloration suggest cross-cultural differences in preferences. These differences were particularly striking for facial yellowness, which had opposite effects on Chinese and White UK participants' face preferences. Importantly, these results do not support the hypothesis that facial color preferences are the same across cultures.

Chapter 5

General Discussion

Many theories of human mate selection and social interaction have suggested that facial appearance functions as a cue of health (e.g. Boothroyd et al., 2013; Coetzee et al., 2007; Lefevre et al., 2013; Rantala et al., 2013a; Whitehead et al., 2012a). In this thesis, I presented three large empirical studies that explored links between social judgments of facial appearance and aspects of underlying physical condition (assessed via hormones and anthropometrics). I also investigated possible cultural influences that may impact the relationship between social judgments of faces and physical-condition cues.

In the first empirical study (Chapter 2), I used a relatively large sample (N=96) to explore the question of whether women's facial appearance signals health information that is indexed by salivary cortisol and/or body mass index (BMI). In this study, I found that none of the facial traits tested (i.e., facial attractiveness, facial dominance, perceived facial health, facial femininity and perceived facial weight/adiposity) were significantly correlated with salivary cortisol. While our results for attractiveness were consistent with Gonzalez-Santoyo et al. (2015), who also found no significant correlation between women's facial attractiveness and cortisol, Rantala et al. (2013a) reported a significant negative correlation between women's facial attractiveness and cortisol. However, by contrast with Gonzalez-Santoyo et al. (2015), we did not find links between women's facial dominance and cortisol. Thus, our null results for both of these traits (among others) call into question the robustness of putative links between cortisol and women's facial appearance.

Additionally, in Chapter 2, we found that women's BMI was negatively and linearly correlated with their facial attractiveness, perceived facial health and facial femininity, and positively and linearly correlated with their facial adiposity. Our results are consistent with previous research suggested that social judgment of women's facial appearance were linked with their body weight (e.g., Coetzee et al.,

2009; Rantala et al., 2013a; Tinlin et al., 2013). Our study is the first study reporting that women's facial femininity is correlated with their BMI.

Women's BMI is linked to their general health (e.g. Brown et al., 2000; Flegal et al., 2005; Ritz and Gardner, 2006), as well as fertility (e.g., Jokela et al., 2008; Pandey et al., 2010; Sallmén et al., 2006). By contrast, cortisol indicates physiological and psychological stress, as well as immunosuppression (Chrousos, 1995; Martin, 2009; Reichlin, 1993; Sapolsky et al., 2000). Thus, the work in my first empirical chapter suggests that women's facial appearance conveys aspects of health that are indexed by women's BMI, rather than cortisol.

In Chapter 3, my second empirical study, I studied the question of whether people can judge men's threat potential/dominance related anthropometrical information (i.e. height, weight and strength) from their faces and/or voices. In this study, we first used principal component analysis to reduce anthropometrics data (e.g., height, weight, strength) to a single threat potential component. We then repeated this principal component analysis for trait ratings of men's faces and, separately, their voices. The analysis produced a single component for each modality that we labelled the perceived facial threat potential component (highly correlated with men's rated strength, rated dominance and rated weight) and perceived vocal threat potential component (highly correlated with men's rated strength, rated dominance and rated weight). These results are consistent with previous research showing that impressions of men's body size, dominance and strength are positively intercorrelated (e.g. Holzleitner & Perrett, 2016), and men's height, weight and strength are positively intercorrelated indices of their threat potential (Puts et al., 2012).

Further analyses suggested that men's perceived facial threat potential component was positively linked to their actual threat potential component and vocal threat potential component. In other words, men whose faces look threatening also have voices that sound threatening and possess physical characteristics that make them a viable source of threat. By contrast, the vocal threat potential component was not

significantly correlated with the actual threat potential component. Our finding of a link between perceived facial threat potential component and actual threat potential component is consistent with previous studies and indicates men's faces contain cues of actual threat potential (Burton & Rule, 2013; Doll et al., 2014; Fink et al., 2007; Hill et al., 2013; Holzleitner & Perrett, 2016; Re et al., 2013; Sell et al., 2009; Windhager et al., 2011). Our results for a link between perceived facial threat potential component and perceived vocal threat potential component is also in line with other research that reported correlations between perceptions of faces and voices (reviewed in Smith et al., 2016) and suggests that men's faces and voices contain certain overlapping information about their perceived threat potential. The lack of a significant correlation between perceived vocal threat potential component and actual threat potential component in our study is not consistent with results reported by Sell et al. (2010), who found a positive association between perceptions of men's voices and measures of their anthropometric data in different cultural populations. However, similar to our results, Doll et al. (2014) found that ratings of men's faces, but not voices, predicted their actual threat potential. These results, together with our own, suggest that men's faces may be a more valid cue to their threat potential/dominance related physical condition than their voices.

Cultural differences may influence the links between social judgments of facial appearance and physical condition. In Chapter 4, the third empirical study, we therefore conducted a cross-cultural study on preferences for facial coloration. We compared Chinese and White UK participants' attractiveness and health judgments of faces on both Chinese and White UK faces. The stimulus faces were independently manipulated in global coloration in three colour dimensions (yellowness, lightness and redness). The results suggest cultural differences between Chinese and White UK participants in their preferences for facial coloration.

For the yellowness dimension, White UK participants preferred faces with increased yellowness as more attractive and healthier than decreased yellowness faces. This is consistent with previous research on White UK participants' judgments of faces (e.g. Stephen et al., 2009a, 2009b, 2011). By contrast, Chinese

participants judged faces with decreased yellowness as more attractive and healthier, rather than increased yellowness faces. For lightness and redness dimensions, both White UK and Chinese participants judged faces with increased lightness or redness as more attractive and healthier than those with decreased lightness or redness, respectively. However, compared to UK participants, Chinese participants showed weaker preference for facial redness and stronger preference for facial lightness. Importantly, these facial colour preferences were similar for judgments of both own-race and other-race faces, which indicates that these cross-cultural differences in preferences are not due to the ethnicity of the target faces (i.e., do not reflect own-race bias in face perception).

White participants showing preferences for increased facial yellowness, redness and lightness is consistent with previous research (Fisher et al., 2014; Kandrik et al., 2017; Stephen et al., 2009a, 2009b, 2011). However, there are only limited cross-cultural studies comparing facial colour preferences between White UK and Black African (Coetzee et al., 2014; Stephen et al., 2012). In studies by Coetzee et al. (2014) and Stephen et al. (2012), both of them found cross-cultural similarity on facial coloration preference between White UK and Black African, whereas we found cross-cultural difference on facial coloration preference between White UK and Chinese. The cultural differences for facial coloration preferences, especially for yellowness, may due to that the links between socioeconomic status and vegetable consumption are inversed between China and UK (Wang, 2001), since facial yellowness could mediated by vegetable consumptions (Foo et al., 2017; Tan et al., 2017; Whitehead et al., 2012). Other factors could also be considered, such as illness prevalence, culture-specific stereotypes. In summary, cultural differences could influence social judgment of face. Similar patterns of results were also in evidence for health judgments, demonstrating that these results are not peculiar to attractiveness judgments.

5.1 Facial Cues of Hormone Levels

Previous studies reported mixed results for relationships between social judgments of women's facial appearances and their cortisol levels. Rantala et al. (2013a)

reported a negative linear relationship between women's cortisol levels and their facial attractiveness. However, Gonzalez-Santoyo et al. (2015) found no links between women's cortisol levels and their facial attractiveness and femininity, whereas they observed a significant negative correlation between women's cortisol levels and their facial dominance. In our larger sample, we found no evidence that women's facial traits that are facial attractiveness, facial dominance, perceived health, femininity and perceived weight/adiposity, were significant correlated with their cortisol levels, which suggested that the links between women's facial appearances and their cortisol levels may not be robust.

Although Rantala et al. (2013a) found a negative association between women's facial attractiveness and cortisol levels, Rantala et al. (2012) did not observe an association between men's facial attractiveness and cortisol levels. Indeed, evidence for links between men's facial appearance and their cortisol levels is equivocal in other studies. For example, while Moore et al. (2011a, 2011b) used composite faces and found men's low cortisol composite faces were preferred more than high cortisol composite faces, the results were not replicated when testing men's composite faces that judged by women from 13 countries (Moore et al., 2013). Moreover, Moore et al. (2011a, 2011b) did not find an association between ratings of men's natural (i.e. non-composite) faces and their cortisol levels. Indeed, a recent study conducted in our lab also did not find significant correlations between men's attractiveness and their cortisol levels (Kandrik et al., 2017).

Previous studies have investigated facial cues of testosterone on men's faces. The results were mixed. While positive associations have been found between male attractiveness related facial traits and testosterone levels (Penton-Voak & Chen, 2004; Roney et al., 2006; Swaddle & Reiersen, 2002; Moore et al., 2011a, 2013; Roney et al., 2016), other studies did not found correlations between male facial traits and testosterone levels (Hönekopp et al., 2007; Neave, Laing, Fink, & Manning, 2003; Pound, Penton-Voak, & Surridge, 2009). The results from the recent study conducted in our lab also showed no association between men's facial attractiveness and their testosterone levels (Kandrik et al., 2017).

In the literatures of human facial attractiveness and mate choice, women's facial attractiveness was hypothesized to signal fertility health, which is indexed by estradiol and/or progesterone (Grammer et al., 2003; Little et al., 2011; Thornhill & Gangestad, 1999). However, empirical evidence that women's facial attractiveness relates to estradiol and/or progesterone is equivocal (Grillot et al., 2014; Jasienska et al., 2004; Law Smith et al., 2006; Puts et al., 2013). A large project was conducted in our lab with a large sample and robust methods (e.g., direct hormone measures from saliva), and we found no evidence that physically attractive women have high estradiol or progesterone (Jones et al., 2017).

The divergent findings for associations between hormones and facial attractiveness could be because there are mediators, such as societal ecology (e.g. societal development index) and/or interaction with other hormones, which could largely impact links between facial appearance and hormones (e.g. Moore et al., 2013). However, from the previous literatures and our results, the associations between facial appearances and hormones are not robust. Differences in results of these associations were frequently observed (e.g. Gonzalez-Santoyo et al., 2015; Han et al., 2016; Moore et al., 2013; Rantala et al., 2013a).

5.2 Methodological Contribution

When testing the relationship between cortisol traits and facial appearances, there are methodological differences between my study and the other two studies (i.e. Rantala et al., 2013; Gonzalez-Santoyo et al., 2015), which may partly explain these inconsistent results. In our lab (i.e. in my study), we collected female participants' salivary cortisol once a week for five weeks (i.e. we can calculate their average cortisol), and at the same time of each day and each week (i.e. we controlled the time of day). This is a very robust and precise way estimating women's traits of cortisol. Cortisol relates to immune response (see Martin, 2009 and Sapolsky et al., 2000 for comprehensive reviews) and is sensitive to both infectious and non-infectious stressors (Chrousos, 1995; Reichlin, 1993), such as body injury and sudden environment changes. Therefore, it would be important to

test cortisol levels that are representative. Rantala et al. (2013a) used “single shot” measure of cortisol (i.e. they measured it only once), which may be noisy and unrepresentative representation of trait cortisol (i.e. average cortisol levels). Although Gonzalez-Santoyo et al. (2015) collected women’s cortisol twice with a thirty minutes gap, they did not control the time of day of collecting salivary cortisol samples.

5.3 Facial and Vocal Cues of Anthropometric Profile

Compared to facial cues of hormone profile, facial cues of anthropometric profile were more robust (reviewed in 1.2 Facial Appearances and Anthropometrics). In the literature, the associations between human anthropometric data (height, weight and strength) and perceived ratings (height, weight and strength) from faces were consistent across studies (*Height*: Burton & Rule, 2013; Re et al., 2012, 2013; Mitteroecker et al., 2013; Schneider et al., 2013; *Weight*: Coetzee et al., 2009; Henderson et al., 2016; Tinlin et al., 2013, *Strength*: Holzleitner & Perrett, 2016; Sell et al., 2009; Toscano et al., 2014).

In Chapter 3, the results showed that people show high inter-rater agreement on judgments of perceived weight, strength and dominance from face. These facial traits were all highly correlated to the perceived facial threat potential component that was positively associated with actual threat potential. This means that individuals’ judgments of men’s facial cues of anthropometric information are consistent with each other, and also reliably linked to actual anthropometric information conveying threat potential. Additionally, face is not only a reliable cue to threat potential, but also a cue to health. In Chapter 2, I found women’s facial adiposity is related to BMI. Facial adiposity, that is perceived weight from face, is positively and linearly associated with BMI (e.g. Coetzee, Perrett, & Stephen, 2009; Tinlin et al., 2013). BMI is often used in medical profession, which was viewed as a health index (e.g. Stommel & Schoenborn, 2010; Jia & Lubetkin, 2005). It has been reported that individuals who fall out off healthy BMI range have increased risks of developing a large number of health problems (e.g., Brown et al., 2000; Wilson et al., 2002; Mokdad et al., 2003; Flegal et al., 2005; Ritz & Gardner, 2006), and who

fall in unhealthy BMI ranges also have low fertility health (e.g., Jokela et al., 2008; Pandey et al., 2010; Sallmén et al., 2006). Indeed, there is growing evidence that facial adiposity is related to actual health (e.g., Coetzee et al., 2014; Tinlin et al., 2013; Rantala et al., 2013b).

Results of Chapter 3 showed that perceived facial threat potential is positively associated with vocal threat potential, which is consistent with other research reporting correlations between perceptions of faces and voices (reviewed in Smith et al., 2016). This suggests that men's faces and voices contain some overlapping information about the perceived threat potential (e.g. social dominance), which was unlikely to include information about their strength, height and weight, however. It is possible that this correlation is driven by cues of men's aggressiveness or emotional state (e.g., anger), rather than threat potential, per se.

Although we observed no evidence for an association between the vocal threat potential component and actual threat potential component, voices have an impact on perceived threat potential. Participants show high inter-rater agreement on perceived weight, strength and dominance from voices. In previous research, low vocal pitch are perceived as dominant and linked to large body size (e.g., Puts et al., 2006; Evans, Neave, & Wakelin, 2006), though a recent work suggests that fundamental frequency and formants frequencies of voices only explain very limited variance in body size (Pisanski et al., 2014). The stereotype of connection between deep voices and a large body size may come from sex differences of relationship between vocal features and body size (i.e. averagely, men tend to have deeper voice and larger body size than women). However, in reality, rather than body size, pubertal expression of sex hormones plays a predominant role in sex differences of vocal pitch (Abitbol et al., 1999; Dabbs, & Mallinger, 1999; Harries, Hawkins, Hacking, & Hughes, 1998; Smith & Patterson, 2005).

Additionally, the voice may convey anthropometric information. However, this is often detected with low accuracy (van Dommelen & Moxness, 1995; Collins, 2000; Lass & Davis, 1976). It was reported in a recent meta-analysis study that

individuals' formant-based vocal tract length estimates explained up to 10% of the variance in height and weight, and F0 explained less than 2% and correlated only weakly with body size within sex (Pisanski et al., 2014). Indeed, results in Chapter 3 show that vocal weight rating is marginally significantly correlated with actual weight ($r=.28$, $N=44$, $p=.063$, uncorrected for multiple comparisons). Large sample sizes may find a weak, but not robust, link between body size and perceived body size from voices. Pisanski et al. (2014) suggested in their meta-analysis review paper that a sample size of at least 99 men would be required to confidently predict height or weight from acoustic properties of formant-based size estimates.

5.4 Cross-Cultural Differences

Early studies investigated social judgments of facial attractiveness in various cultures and claimed that people show agreement on general facial attractiveness judgments (e.g. Cunningham, Roberts, Barbee, Druen, & Wu, 1995). Other studies reported systematic variation in social judgments of facial attractiveness (Honekopp, 2006; Penton-Voak, Jacobson, & Trivers, 2004; Scott et al., 2014). Indeed, many studies have suggested that mate preference and social judgments of facial attractiveness can be influenced by social ecology, such as prevalence of pathogens (DeBruine, Little, & Jones, 2012; Gangestad & Buss, 1993; Jones et al., 2013), human development index (Moore et al., 2013), national income inequality (Brooks et al., 2011) and prevalence of violence exposure (Borras-Guevara et al., 2017). Consistent with these findings, in my third empirical chapter, I found cultural differences in preferences for facial coloration. There are two caveats to this study, however. First, we used global color manipulations of faces, but did not consider the effects of color distribution (Fink & Matts, 2008). Second, in our stimuli faces, we only manipulated facial color, but not shape changes. Color information may not influence facial attractiveness when other facial cues also vary in image sets (Foo et al., 2017a).

5.5 Facial Cues of Health

More work is needed to investigate facial cues of health. In Chapter 2, I investigated a possible association between women's facial appearance and their cortisol level. Although in the study cortisol was viewed as a health index, there are many other physiological parameters that could be investigated as health indexes. For example, links between frequency of illness and facial appearances (e.g. Kalick et al., 1998; Shackelford et al., 1999; Gray et al., 2012; Boothroyd et al., 2013), links between MHC and facial preferences (e.g. Lie et al., 2010; Thornhill et al., 2003; Roberts et al., 2005) and links between immune function and facial appearances (e.g. Rantala et al., 2012, 2013a, 2013b; Skrinda et al., 2014; Foo et al., 2017a) may reveal associations between attractiveness and health not apparent in the current studies.

5.6 Conclusion

The theory that facial appearance conveys cues of health, anthropometric profiles and hormone profiles, leading to universal preferences for certain facial cues has become highly influential. In my thesis, I found links between women's BMI and their facial appearance were more robust than those assumed to occur between cortisol levels and facial appearance. I also found that men's threat potential (as indexed by anthropometric profile) was linked to faces, but not voices. These results indicate that links between facial appearance and aspects of health that are indexed by cortisol (e.g., immune responses) may be overstated in the literature, while links between facial appearances and anthropometric profile may be more robust. I also showed that facial color preferences can differ between cultures in ways that cannot be explained by own-race biases. This latter finding is important, since it challenges the assumption that preferences for health cues are universal.

References

- Abel, E. L., & Kruger, M. L. (2010). Smile intensity in photographs predicts longevity. *Psychological Science*, 21(4), 542-544.
- Abitbol, J., Abitbol, P., & Abitbol, B. (1999). Sex hormones and the female voice. *Journal of voice*, 13(3), 424-446.
- Adolphs, R. (2001). The neurobiology of social cognition. *Current Opinion in Neurobiology*, 11(2), 231-239.
- Alaluf, S., Heinrich, U., Stahl, W., Tronnier, H., & Wiseman, S. (2002). Dietary carotenoids contribute to normal human skin color and UV photosensitivity. *The Journal of nutrition*, 132(3), 399-403.
- Alexander, J., & Stimson, W. H. (1988). Sex hormones and the course of parasitic infection. *Parasitology Today*, 4(7), 189-193.
- Alexander, M., Newmark, H., & Miller, R. G. (1985). Oral beta-carotene can increase the number of OKT4+ cells in human blood. *Immunology letters*, 9(4), 221-224.
- Altemus, M., Redwine, L., Leong, Y. M., Yoshikawa, T., Yehuda, R., Detera-Wadleigh, S., & Murphy, D. L. (1997). Reduced sensitivity to glucocorticoid feedback and reduced glucocorticoid receptor mRNA expression in the luteal phase of the menstrual cycle. *Neuropsychopharmacology*, 17(2), 100-109.
- Andersson, M. B. (1994). *Sexual selection*. Princeton University Press, Princeton.
- Apanius, V., Penn, D., Slev, P. R., Ruff, L. R., & Potts, W. K. (1997). The nature of selection on the major histocompatibility complex. *Critical Reviews™ in Immunology*, 17(2).
- Barba, C., Cavalli-Sforza, T., Cutter, J., & Darnton-Hill, I. (2004). Appropriate body-mass index for Asian populations and its implications for policy and intervention strategies. *The lancet*, 363(9403), 157.
- Barr, D. J. (2013) Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology*, 4, 328.
doi:10.3389/fpsyg.2013.00328
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68, 255-278.

-
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1-48.
- Bestelmeyer, P. E., Latinus, M., Bruckert, L., Rouger, J., Crabbe, F., & Belin, P. (2012). Implicitly perceived vocal attractiveness modulates prefrontal cortex activity. *Cerebral Cortex*, 22(6), 1263-1270.
- Bird, B. M., Jofré, V. S. C., Geniole, S. N., Welker, K. M., Zilioli, S., Maestripieri, D., ... & Carré, J. M. (2016). Does the facial width-to-height ratio map onto variability in men's testosterone concentrations?. *Evolution and Human Behavior*, 37(5), 392-398.
- Bleske-Rechek, A., Harris, H. D., Denking, K., Webb, R. M., Erickson, L., & Nelson, L. A. (2011). Physical cues of ovulatory status: A failure to replicate enhanced facial attractiveness and reduced waist-to-hip ratio at high fertility. *Evolutionary Psychology*, 9(3), 147470491100900306.
- Bobst, C., & Lobmaier, J. S. (2012). Men's preference for the ovulating female is triggered by subtle face shape differences. *Hormones and behavior*, 62(4), 413-417.
- 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.
- Boothroyd L. G., Lawson J. F., and Burt D. M. (2009). Testing immunocompetence explanations of male facial masculinity. *Journal of Evolutionary Psychology*, 7, 65–81.
- Boothroyd, L. G., Scott, I., Gray, A. W., Coombes, C. I., & Pound, N. (2013). Male facial masculinity as a cue to health outcomes. *Evolutionary psychology*, 11(5), 147470491301100508.
- Borras-Guevara, M. L., Batres, C., & Perrett, D. I. (2017). Aggressor or protector? Experiences and perceptions of violence predict preferences for masculinity. *Evolution and Human Behavior*.
- Brooks, R., Scott, I. M., Maklakov, A. A., Kasumovic, M. M., Clark, A. P., & Penton-Voak, I. S. (2010). National income inequality predicts women's preferences for masculinized faces better than health does. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20100964.

-
- Brown, W. J., Mishra, G., Kenardy, J., & Dobson, A. (2000). Relationships between body mass index and well-being in young Australian women. *International journal of obesity*, 24(10), 1360.
- Buechner, V. L., Maier, M. A., Lichtenfeld, S., & Elliot, A. J. (2015). Emotion expression and color: Their joint influence on perceived attractiveness and social position. *Current Psychology*, 34(2), 422-433.
- Burton, C. M., & Rule, N. O. (2013). Judgments of height from faces are informed by dominance and facial maturity. *Social Cognition*, 31(6), 672-685.
- Burrows, R., Correa-Burrows, P., Reyes, M., Blanco, E., Albala, C., & Gahagan, S. (2017). Low muscle mass is associated with cardiometabolic risk regardless of nutritional status in adolescents: A cross-sectional study in a Chilean birth cohort. *Pediatric Diabetes*.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: an evolutionary perspective on human mating. *Psychological review*, 100(2), 204.
- Calle, E. E., Thun, M. J., Petrelli, J. M., Rodriguez, C. & Heath, C. W. (1999). Body-mass index and mortality in a prospective cohort of U.S. adults. *New England Journal of Medicine*, 341, 1097-1105.
- Christensen, K., Thinggaard, M., McGue, M., Rexbye, H., Aviv, A., Gunn, D., ... & Vaupel, J. W. (2009). Perceived age as clinically useful biomarker of ageing: cohort study. *British Medical Journal*, 339, b5262.
- Chrousos, G. P. (1995). The hypothalamic–pituitary–adrenal axis and immune-mediated inflammation. *New England Journal of Medicine*, 332(20), 1351-1363.
- Coetzee, V., Barrett, L., Greeff, J. M., Henzi, S. P., Perrett, D. I., & Wade, A. A. (2007). Common HLA alleles associated with health, but not with facial attractiveness. *PLoS One*, 2(7), e640.
- Coetzee, V., Perrett, D. I., & Stephen, I. D. (2009). Facial adiposity: a cue to health?. *Perception*, 38(11), 1700-1711.
- 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(2), 190-193.
- 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

-
- Coetzee, V., & Perrett, D. I. (2014). Effect of beta-carotene supplementation on African skin. *Journal of biomedical optics*, 19(2), 025004.
- 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
- Collins, S. A. (2000). Men's voices and women's choices. *Animal behaviour*, 60(6), 773-780.
- Commission Internationale de L'Éclairage. (1976). CIE Colorimetry – Part 4: 1976 L*a*b* Color Space.
- Courtiol, A., Raymond, M., Godelle, B., & Ferdy, J. B. (2010). Mate choice and human stature: Homogamy as a unified framework for understanding mating preferences. *Evolution*, 64, 2189–2203.
- Cunningham, M. R., Roberts, A. R., Barbee, A. P., Druen, P. B., & Wu, C.-H. (1995). " Their ideas of beauty are, on the whole, the same as ours": Consistency and variability in the cross-cultural perception of female physical attractiveness. *Journal of personality and social psychology*. 68(2), 261.
- Da Silva, J. A. P. (1999). Sex hormones and glucocorticoids: Interactions with the immune system. *Annals of the New York Academy of Sciences*, 22, 102-117.
- Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low voice pitch among men. *Personality and individual differences*, 27(4), 801-804.
- Daniels, F. J. W., van der Leun, K. C., & Johnson, B. E. (1973). Sunburn. In C. L. Brace & J. Metress (Eds.), *Man in Evolutionary Perspective*. Toledo.
- DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L., & Little, A. C. (2010). The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society of London B: Biological Sciences*, 277(1692), 2405-2410.
- DeBruine, L. M., Little, A. C., & Jones, B. C. (2012). Extending parasite-stress theory to variation in human mate preferences. *Behavioral and Brain Sciences*, 35(2), 86-87.
- Dixson, A. F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. Oxford University Press, Oxford.

-
- Dixson, B. J., Lee, A. J., Sherlock, J. M., & Talamas, S. N. (2017). Beneath the beard: do facial morphometrics influence the strength of judgments of men's beardedness?. *Evolution and Human Behavior*, 38(2), 164-174.
- Doherty, P. C. & Zinkernagel, R. M. 1975 Enhanced immunological surveillance in mice heterozygous at the H-2 gene complex. *Nature*. 256, 50-52.
- Doll, L. M., Hill, A. K., Rotella, M. A., Cárdenas, R. A., Welling, L. L., Wheatley, J. R., & Puts, D. A. (2014). How well do men's faces and voices index mate quality and dominance?. *Human Nature*, 25, 200-212.
- Dowling, D. K., & Simmons, L. W. (2009). Reactive oxygen species as universal constraints in life-history evolution. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb-2008.
- Dubuc, C., Brent, L. J., Accamando, A. K., Gerald, M. S., MacLarnon, A., Semple, S., ... & Engelhardt, A. (2009). Sexual skin color contains information about the timing of the fertile phase in free-ranging *Macaca mulatta*. *International Journal of Primatology*, 30(6), 777-789.
- Edwards, E. A., & Duntley, S. Q. (1939). The pigments and color of living human skin. *American Journal of Anatomy*, 65(1), 1-33.
- Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6), 581-604.
- Enlow, D. M. 1982 *Handbook of facial growth*, 2nd edn. Philadelphia, PA: Saunders.
- Enlow, D. H., and Hans, M. G. (1996). *Essentials of facial growth*. US: Harcourt.
- Evans, S., Neave, N., & Wakelin, D. (2006). Relationships between vocal characteristics and body size and shape in human males: an evolutionary explanation for a deep male voice. *Biological psychology*, 72(2), 160-163.
- Farvid, M. S., Ng, T. W. K., Chan, D. C., Barrett, P. H. R., & Watts, G. F. (2005). Association of adiponectin and resistin with adipose tissue compartments, insulin resistance and dyslipidaemia. *Diabetes, obesity and metabolism*, 7(4), 406-413.
- Feinberg, D. R., Jones, B. C., Smith, M. L., Moore, F. R., DeBruine, L. M., Cornwell, R. E., ... & Perrett, D. I. (2006). Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Hormones and behavior*, 49(2), 215-222.

-
- Fiedor, J., & Burda, K. (2014). Potential role of carotenoids as antioxidants in human health and disease. *Nutrients*, 6(2), 466-488.
- Fink, B., Neave, N., & Seydel, H. (2007). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, 19(1), 82-87.
- Fink, B., & Matts, P. J. (2008). The effects of skin colour distribution and topography cues on the perception of female facial age and health. *Journal of the European Academy of Dermatology and Venereology*, 22(4), 493-498.
- 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(4), 474-485.
- Fisher CI, Hahn AC, Debruine LM, Jones BC. (2014) Integrating shape cues of adiposity and color information when judging facial health and attractiveness. *Perception* 43, 499–508.
- Flegal, K. M., Graubard, B. I., Williamson, D. F., & Gail, M. H. (2005). Excess deaths associated with underweight, overweight, and obesity. *The Journal of the American Medical Association*, 293(15), 1861-1867.
- Flinn, M. V. (2009). Are cortisol profiles a stable trait during child development? *American Journal of Human Biology*, 21, 769–771.
- Folstad, I. and Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139, 603-622.
- Foo, Y. Z., Nakagawa, S., Rhodes, G., & Simmons, L. W. (2016). The effects of sex hormones on immune function: a meta-analysis. *Biological Reviews*. 92 (1), 551-571.
- Foo, Y. Z., Simmons, L. W., & Rhodes, G. (2017a). Predictors of facial attractiveness and health in humans. *Scientific Reports*, 7.
- Foo, Y. Z., Rhodes, G., & Simmons, L. W. (2017b). The carotenoid beta-carotene enhances facial color, attractiveness and perceived health, but not actual health, in humans. *Behavioral Ecology*.
- Forbes, G.B. (1975) *Puberty: Body composition*. In Puberty (Berenson, S.R., ed.), pp. 132–145, Leiden.
- Freedman, D. S., Wang, J., Maynard, L. M., Thornton, J. C., Mei, Z., Pierson, R. N., ... & Horlick, M. (2005). Relation of BMI to fat and fat-free mass among children and adolescents. *International journal of obesity*, 29(1), 1.

-
- Galton, F. (1879). Composite Portraits, Made by Combining Those of Many Different Persons Into a Single Resultant Figure. *The Journal of the Anthropological Institute of Great Britain and Ireland*, 8, 132-144.
- Gangestad, S. W. & Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral & Brain Sciences*, 23, 573-587.
- Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior*, 24(4), 231-241.
- Gangestad, S. W. & Scheyd, G. J. 2005 The evolution of human physical attractiveness. *Annu. Rev. Anthropol.* 34, 523-548.
- Gangestad, S. W., & Haselton, M. G. (2015). Human estrus: implications for relationship science. *Current Opinion in Psychology*, 1, 45-51.
- Geniole, S. N., Denson, T. F., Dixson, B. J., Carré, J. M., & McCormick, C. M. (2015). Evidence from meta-analyses of the facial width-to-height ratio as an evolved cue of threat. *PloS one*, 10(7), e0132726.
- Geraedts E.J., van Dommelen P., Caliebe J., Visser R., Ranke M.B., van Buuren S., Wit J.M., Oostdijk W., 2011. Association between head circumference and body size. *Horm. Res. Paediatr.* 75(3): 213–219.
- 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.
- Gray, A. W., & Boothroyd, L. G. (2012). Female facial appearance and health. *Evolutionary Psychology*, 10(1).
- Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *J. Comp. Psychol.* 108, 233–242.
- Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews*, 78, 385 – 407.
- Grillot, R. L., Simmons, Z. L., Lukaszewski, A. W., & Roney, J. R. (2014). Hormonal and morphological predictors of women's body attractiveness. *Evolution and Human Behavior*, 35, 176-183.

-
- Hagen, T. M. et al. (1994). Extensive oxidative DNA damage in hepatocytes of transgenic mice with chronic active hepatitis destined to develop hepatocellular carcinoma. *Proc. Natl. Acad. Sci. USA* 91, 12808–12812.
- Halliwell, B. (2000). Lipid peroxidation, antioxidants and cardiovascular disease: How should we move forward? *Cardiovasc. Res.* 47, 410–418.
- 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(3), 352-355.
- Harbuz, M. S., & Lightman, S. L. (1992). Stress and the hypothalamo-pituitary-adrenal axis: acute, chronic and immunological activation. *Journal of Endocrinology*, 134(3), 327-339.
- Harries, M., Hawkins, S., Hacking, J., & Hughes, I. (1998). Changes in the male voice at puberty: vocal fold length and its relationship to the fundamental frequency of the voice. *The Journal of Laryngology & Otology*, 112(5), 451-454.
- Haselton, M. G., & Gildersleeve, K. (2016). Human ovulation cues. *Current Opinion in Psychology*, 7, 120-125.
- Havlicek, J. & Roberts, S. C. 2009 MHC-correlated mate choice in humans: A review. *Psyneuen*. 34, 497 – 512.
- Havlicek, J., Cobey, K. D., Barrett, L., Klapilová, K., & Roberts, S. C. (2015). The spandrels of Santa Barbara? A new perspective on the peri-ovulation paradigm. *Behavioral Ecology*, 26, 1249-1260.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in cognitive sciences*, 4(6), 223-233.
- Henderson, J. J., & Anglin, J. M. (2003). Facial attractiveness predicts longevity. *Evolution and human behavior*, 24(5), 351-356.
- Henderson, A. J., Holzleitner, I. J., Talamas, S. N., & Perrett, D. I. (2016). Perception of health from facial cues. *Phil. Trans. R. Soc. B*, 371(1693), 20150380.
- Henderson, A. J., Lasselin, J., Lekander, M., Olsson, M. J., Powis, S. J., Axelsson, J., & Perrett, D. I. (2017). Skin colour changes during experimentally-induced sickness. *Brain, Behavior & Immunity*, 60, 312-318.
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010a). Most people are not WEIRD. *Nature*, 466(7302), 29-29.

-
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010b). The weirdest people in the world? *Behavioral and brain sciences*, 33(2-3), 61-83.
- Hill, A. K., Hunt, J., Welling, L. L., Cárdenas, R. A., Rotella, M. A., Wheatley, J. R., ... & Puts, D. A. (2013). Quantifying the strength and form of sexual selection on men's traits. *Evolution and Human Behavior*, 34(5), 334-341.
- Hodges-Simeon, C. R., Gurven, M., Puts, D. A., & Gaulin, S. J. C. (2014). Vocal fundamental and formant frequencies are honest signals of threat potential in peripubertal males. *Behavioral Ecology*, 25, 984–988.
- Holzleitner, I. J., Hunter, D. W., Tiddeman, B. P., Seck, A., Re, D. E., & Perrett, D. I. (2014). Men's facial masculinity: When (body) size matters. *Perception*, 43(11), 1191-1202.
- Holzleitner, I. J., & Perrett, D. I. (2016). Perception of strength from 3D faces is linked to facial cues of physique. *Evolution and Human Behavior*, 37(3), 217-229.
- Hönekopp, J., Bartholomé, T., & Jansen, G. (2004). Facial attractiveness, symmetry, and physical fitness in young women. *Human Nature*, 15(2), 147-167.
- Hönekopp, J., Rudolph, U., Beier, L., Liebert, A., & Müller, C. (2007). Physical attractiveness of face and body as indicators of physical fitness in men. *Evolution and Human Behavior*, 28(2), 106-111.
- Hong, G., Luo, M. R., & Rhodes, P. A. (2001). A study of digital camera colorimetric characterization based on polynomial modeling. *Color Research & Application*, 26, 76–84.
- Hoyme, H. E. (1993). Minor anomalies: diagnostic clues to aberrant human morphogenesis. *Genetica*, 89(1), 307-315.
- Hubert, H. B., Feinleib, M., McNamara, P. M., & Castelli, W. P. (1983). Obesity as an independent risk factor for cardiovascular disease: a 26-year follow-up of participants in the Framingham Heart Study. *Circulation*, 67(5), 968-977.
- Hughes, D. A. (2001). Dietary carotenoids and human immune function. *Nutrition*, 17(10), 823-827.
- Hume, D. & Montgomerie, R. (2001). Facial attractiveness signals different aspects of “quality” in women and men. *Evolution & Human Behavior*, 22, 93-112.
- Jasienska G., Ziomkiewicz A., Ellison P. T., Lipson S. F., & Thune I. (2004). Large breast and narrow waist indicate high reproductive potential in women.

Proceedings of the Royal Society of London B: Biological Sciences, 271, 1213–1217.

- Jia, H., & Lubetkin, E. I. (2005). The impact of obesity on health-related quality-of-life in the general adult US population. *Journal of public health*, 27(2), 156-164.
- 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.
- Johnston, V. S. (2006). Mate choice decisions: the role of facial beauty. *Trends in cognitive sciences*, 10(1), 9-13.
- Jokela, M., Elovainio, M., & Kivimäki, M. (2008). Lower fertility associated with obesity and underweight: the US National Longitudinal Survey of Youth. *The American journal of clinical nutrition*, 88(4), 886-893.
- 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.
- Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L. G., Cornwell, R. E., Feinberg, D. R., Tiddeman, B. P., Whiten, S., Pitman, R. M., Hillier, S. G., Burt, D. M., Stirrat, M. R., Law Smith, M. J. & Moore, F. R. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London B*, 272, 347-354.
- Jones, B. C., DeBruine, L. M., Little, A. C., Burriss, R. P., & Feinberg, D. R. (2007). Social transmission of face preferences among humans. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1611), 899-903.
- Jones, B. C., DeBruine, L. M., Perrett, D. I., Little, A. C., Feinberg, D. R., & Smith, M. J. L. (2008). Effects of menstrual cycle phase on face preferences. *Archives of sexual behavior*, 37(1), 78-84.
- Jones, B. C., Fincher, C. L., Welling, L. L., Little, A. C., Feinberg, D. R., Watkins, C. D., ... & DeBruine, L. M. (2013). Salivary cortisol and pathogen disgust predict men's preferences for feminine shape cues in women's faces. *Biological Psychology*, 92(2), 233-240.

-
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wincenciak, J., Kandrik, M., Roberts, S. C., ... & DeBruine, L. M. (2015). Facial coloration tracks changes in women's estradiol. *Psychoneuroendocrinology*, *56*, 29-34.
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., ... & DeBruine, L. M. (2017). Within-Woman Hormone-Attractiveness Correlations Are Not Simply Byproducts Of Between-Women Hormone-Attractiveness Correlations. *BioRxiv*, 136515.
- Judge, T. A., & Cable, D. M. (2004). The effect of physical height on workplace success and income: Preliminary test of a theoretical model. *Journal of Applied Psychology*, *89*, 428–441.
- 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*, 8–13.
- Kandrik, M., Hahn, A. C., Wincenciak, J., Fisher, C. I., Pisanski, K., Feinberg, D. R., Lisa DeBruine, L. M., Jones, B. C. (2016). Are men's perceptions of sexually dimorphic vocal characteristics related to their testosterone levels? Paper presented at *HBES 2016*, Vancouver (USA).
- Kandrik, M., Hahn, A. C., Han, C., Wincenciak, J., Fisher, C. I., DeBruine, L. M., & Jones, B. C. (2017). Does the Interaction Between Cortisol and Testosterone Predict Men's Facial Attractiveness?. *Adaptive Human Behavior and Physiology*, 1-7.
- Kandrik, M., Hahn, A. C., Fisher, C., Wincenciak, J., DeBruine, L. M. & Jones, B. C. (2017). Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences. *Hormones & Behavior*, *87*, 57-61.
- Keeley, L. H. (1996). *War before civilization*. Oxford University Press.
- Kirkpatrick M, Ryan MJ. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* *350*, 33–38.
- Koehler, N., Simmons, L. W., Rhodes, G., & Peters, M. (2004). The relationship between sexual dimorphism in human faces and fluctuating asymmetry. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*(Suppl 4), S233-S236.
- Koulack, D., & Tuthill, J. A. (1972). Height perception: A function of social distance. *Canadian Journal of Behavioural Science*, *4*, 50–53.

-
- Kowner, R. (1996). Facial asymmetry and attractiveness judgement in developmental perspective. *Journal of Experimental Psychology: Human Perception and Performance*, 22(3), 662.
- Kramer, R. S., Gottwald, V. M., Dixon, T. A., & Ward, R. (2012). Different cues of personality and health from the face and gait of women. *Evolutionary Psychology*, 10(2), 147470491201000208.
- Krupp, D. B., DeBruine, L. M., & Jones, B. C. (2011). Apparent health encourages reciprocity. *Evolution and Human Behavior*, 32(3), 198-203.
- Krupp, D. B., DeBruine, L. M., Jones, B. C. & Lalumière, M. L. (2012). Kin recognition: Evidence for the perception of both positive and negative relatedness. *Journal of Evolutionary Biology*, 25, 1472-1478.
- Kurzban, R., & Weeden, J. (2005). HurryDate: Mate preferences in action. *Evolution and Human Behavior*, 26, 227–244.
- Laakso, M., Matilainen, V., & Keinänen-Kiukaanniemi, S. (2002). Association of neck circumference with insulin resistance-related factors. *International journal of obesity*, 26(6), 873.
- Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological science*, 1(2), 115-121.
- 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, 390-423.
- Lass, N. J., & Davis, M. (1976). An investigation of speaker height and weight identification. *The Journal of the Acoustical Society of America*, 60(3), 700-703.
- Latinus, M., & Belin, P. (2011). Anti-voice adaptation suggests prototype-based coding of voice identity. *Frontiers in psychology*, 2.
- Latinus, M., McAleer, P., Bestelmeyer, P. E., & Belin, P. (2013). Norm-based coding of voice identity in human auditory cortex. *Current Biology*, 23(12), 1075-1080.
- Law-Smith, M. J., Perrett, D. I., Jones, B. C., Cornwell, R. E., Moore, F. R., Feinberg, D. R., Boothroyd, L. G., Durrani, S. J., Stirrat, M. R., Whiten, S., Pitman, R. M., and Hillier, S.G. (2006). Facial appearance is a cue to oestrogen levels in women. *Proceedings of the Royal Society B-Biological Sciences*, 273, 135-140.

-
- 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*(6), 20130633.
- Lefevre, C. E., Lewis, G. J., Perrett, D. I., & Penke, L. (2013). Telling facial metrics: facial width is associated with testosterone levels in men. *Evolution and Human Behavior*, *34*(4), 273-279.
- Leong, D. P., Teo, K. K., Rangarajan, S., Lopez-Jaramillo, P., Avezum, A., Orlandini, A., ... & Rahman, O. (2015). Prognostic value of grip strength: findings from the Prospective Urban Rural Epidemiology (PURE) study. *The Lancet*, *386*(9990), 266-273.
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature neuroscience*, *4*(1), 89.
- Levine, J. A., Ray, A., & Jensen, M. D. (1998). Relation between chubby cheeks and visceral fat. *New England Journal of Medicine*, *339*(26), 1946-1947.
- Loomis, W. F. (1967). Skin-pigment regulation of vitamin-D biosynthesis in man. *Science*, *157*(788), 501-506.
- Lorentzon, M., Swanson, C., Andersson, N., Mellström, D., & Ohlsson, C. (2005). Free testosterone is a positive, whereas estradiol is a negative, predictor of cortical bone size in young Swedish men: The GOOD study. *Journal of Bone and Mineral Research*, *20*, 1334–1341.
- Lozano, G. A. (1994). Carotenoids, parasites, and sexual selection. *Oikos* *70*, 309–311.
- Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution*, *62*(10), 2473-2486.
- Lie, H. C. (2009). *The role of genetic diversity in human sexual selection: is the MHC special?* (Doctoral dissertation, University of Western Australia).
- Lie, H. C., Simmons, L. W., & Rhodes, G. (2010). Genetic dissimilarity, genetic diversity, and mate preferences in humans. *Evolution and Human Behavior*, *31*(1), 48-58.
- Little, A. C. & Jones, B. C. (2003). Evidence against perceptual bias views for symmetry preferences in human faces. *Proc. R. Soc. Lond. B* *270*, 1759–1763.

-
- Little, A. C. & Jones, B. C. (2006). Attraction independent of detection suggests special mechanisms for symmetry preferences in human face perception. *Proc. R. Soc. B* 273, 3093–3099.
- 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. *Proc. R. Soc. B* 274, 3113–3117.
- Little, A. C., Cohen, D. L., Jones, B. C., & Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. *Behavioral Ecology and Sociobiology*, 61(6), 967-973.
- Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies change across the menstrual cycle. *Hormones and Behavior*, 51(5), 633-639.
- Little, A. C., Jones, B. C., DeBruine, L. M., & Feinberg, D. R. (2008). Symmetry and sexual dimorphism in human faces: interrelated preferences suggest both signal quality. *Behavioral Ecology*, 19(4), 902-908.
- Little, A. C., Jones, B. C. & DeBruine, L. M. (2011). Facial attractiveness: Evolutionary based research. *Philosophical Transactions of the Royal Society B*, 366, 1638-1659.
- Little, A. C., Třebický, V., Havlíček, J., Roberts, S. C. & Kleisner, K. (2015). Human perception of fighting ability: Facial cues predict winners and losers in mixed martial arts fights. *Behavioral Ecology*, 26, 1470-1475.
- Livshits, G., & Kobyliansky, E. (1991). Fluctuating asymmetry as a possible measure of developmental homeostasis in humans: a review. *Human Biology*, 441-466.
- Luevano, V. X. (2007) Truth in advertising: The relationship of facial appearance to apparent and actual health across the lifespan. PhD dissertation. Brandeis University.
- Mackay, N. J. (2010). Scaling of human body mass with height: The body mass index revisited. *Journal of biomechanics*, 43(4), 764-766.
- Manson, J. H., Wrangham, R. W., Boone, J. L., Chapais, B., Dunbar, R. I. M., Ember, C. R., ... & Paterson, J. D. (1991). Intergroup aggression in chimpanzees and humans. *Current anthropology*, 32, 369-390.

-
- Manson, J. E., Willett, W. C., Stampfer, M. J., Colditz, G. A., Hunter, D. J., Hankinson, S. E., ... & Speizer, F. E. (1995). Body weight and mortality among women. *New England Journal of Medicine*, 333(11), 677-685.
- Manning, J. T., & Scutt, D. (1996). Symmetry and ovulation in women. *Human Reproduction*, 11(11), 2477-2480.
- Martin, L. B. (2009). Stress and immunity in wild vertebrates: timing is everything. *General and comparative endocrinology*, 163(1), 70-76.
- Mayer, C., Windhager, S., Schaefer, K., & Mitteroecker, P. (2017). BMI and WHR Are Reflected in Female Facial Shape and Texture: A Geometric Morphometric Image Analysis. *PLoS One*, 12(1), e0169336.
- McAleer, P., Todorov, A., & Belin, P. (2014). How do you say 'Hello'? Personality impressions from brief novel voices. *PloS one*, 9(3), e90779.
- McCann, S. J. H. (2001). Height, societal threat, and the victory margin in presidential elections (1824–1992). *Psychological Reports*, 88, 741–742.
- Mehta, P. H., DesJardins, N. M. L., van Vugt, M., & Josephs, R. A. (2017). Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game. *Hormones and Behavior*.
- Meyer, H. E., & Selmer, R. (1999). Income, educational level and body height. *Annals of Human Biology*, 26, 219–227.
- Meredith, P., & Riesz, J. (2004). Radiative relaxation quantum yields for synthetic eumelanin. *Photochemistry and photobiology*, 79(2), 211-216.
- Mitteroecker, P., Gunz, P., Windhager, S., & Schaefer, K. (2013). A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. *Hystrix, the Italian Journal of Mammalogy*, 24(1), 59-66.
- Mitton, J. B., & Grant, M. C. (1984). Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annual review of ecology and systematics*, 15(1), 479-499.
- Mokdad, A. H., Ford, E. S., Bowman, B. A., Dietz, W. H., Vinicor, F., Bales, V. S., & Marks, J. S. (2003). Prevalence of obesity, diabetes, and obesity-related health risk factors, 2001. *The Journal of the American Medical Association*, 289(1), 76-79.

-
- Mokdad, A. H., Marks, J. S., Stroup, D. F., & Gerberding, J. L. (2004). Actual causes of death in the United States, 2000. *Journal of the American Medical Association*, 291(10), 1238–1245.
- Møller, A. P. 1997 Developmental stability and fitness: a review. *Am. Nat.* 149, 916–932.
- Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, developmental stability and evolution*. Oxford University Press, UK.
- Møller, A. P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: a meta-analysis. *The American Naturalist*, 151(2), 174-192.
- Monk, B. (1983). Carotenemia. *International Journal of Dermatology*, 22(6), 376-377.
- 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
- Moore, F. R., Al Dujaili, E. A., Cornwell, R. E., Smith, M. L., 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(3), 269-274.
- Moore, F. R., Cornwell, R. E., Smith, M. L., Al Dujaili, E. A., 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: Biological Sciences*, rspb20101678.
- Moore, F. R., Coetzee, V., Contreras-Garduño, J., Debruine, L. M., Kleisner, K., Krams, I., ... & Schaum, N. (2013). Cross-cultural variation in women's preferences for cues to sex-and stress-hormones in the male face. *Biology Letters*, 9(3), 20130050.
- Morrow, L. E., McClellan, J. L., Conn, C. A., Kluger, M. J. (1993). Glucocorticoids alter fever and IL-6 responses to psychological stress and to lipopolysaccharide. *American Journal of Physiology*, 264, R1010 –R1016.
- Milinski, M. (2006). The major histocompatibility complex, sexual selection, and mate choice. *Annu. Rev. Ecol. Evol. Syst.*, 37, 159-186.
- Muehlenbein, M. P., & Bribiescas, R. G. (2005). Testosterone-mediated immune functions and male life histories. *American Journal of Human Biology*, 17(5), 527-558.

-
- Murray, F. G. (1934). Pigmentation, sunlight and nutritional disease. *American Anthropologist*, 36(3), 438-448.
- Murray, G. R., & Schmitz, J. D. (2011). Caveman politics: Evolutionary leadership preferences and physical stature. *Social Science Quarterly*, 92, 1215–1235.
- Must, A., Spadano, J., Coakley, E. H., Field, A. E., Colditz, G., & Dietz, W. H. (1999). The disease burden associated with overweight and obesity. *The Journal of the American Medical Association*, 282(16), 1523-1529.
- Neave N., Laing, S., Fink, B., Manning, J. T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proceedings of the Royal Society B*, 270, 2167 – 2172.
- Newman, A. B., Kupelian, V., Visser, M., Simonsick, E. M., Goodpaster, B. H., Kritchevsky, S. B., ... & Harris, T. B. (2006). Strength, but not muscle mass, is associated with mortality in the health, aging and body composition study cohort. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, 61(1), 72-77.
- Oberzaucher, E., & Grammer, K. (2009). Immune reactivity and attractiveness. *Gerontology*, 56(6), 521-524.
- Oberzaucher, E., Katina, S., Schmehl, S. F., Holzleitner, I. J., Mehu-Blantar, I., & Grammer, K. (2012). The myth of hidden ovulation: Shape and texture changes in the face during the menstrual cycle. *Journal of Evolutionary Psychology*, 10(4), 163-175.
- Pandey, S., Pandey, S., Maheshwari, A., & Bhattacharya, S. (2010). The impact of female obesity on the outcome of fertility treatment. *Journal of human reproductive sciences*, 3(2), 62.
- Papacosta, E., & Nassis, G. P. (2011). Saliva as a tool for monitoring steroid, peptide and immune markers in sport and exercise science. *Journal of Science and Medicine in Sport*, 14(5), 424-434.
- Pawlowski, B., & Koziel, S. (2002). The impact of traits offered in personal advertisements on response rates. *Evolution and Human Behavior*, 23, 139–149.
- Penn, D. J., Damjanovich, K., & Potts, W. K. (2002). MHC heterozygosity confers a selective advantage against multiple-strain infections. *Proceedings of the National Academy of Sciences*, 99(17), 11260-11264.

-
- 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.
- Penton-Voak, I. S. & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, 25, 229 – 241.
- Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgments of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior*, 25(6), 355-370.
- 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.
- Phalane, K. G., Tribe, C., Steel, H. C., Cholo, M. C. & Coetzee, V. (2017). Facial appearance reveals immunity in African men. *Scientific Reports*, 7, 7443.
- Piertney, S. B. & Oliver, M. B. (2006). The evolutionary ecology of the major histocompatibility complex. *Heredity*. 96, 7-21.
- Pisanski, K., Fraccaro, P. J., Tigue, C. C., O'Connor, J. J., Röder, S., Andrews, P. W., ... & Feinberg, D. R. (2014). Vocal indicators of body size in men and women: a meta-analysis. *Animal Behaviour*, 95, 89-99.
- Pisanski, K., Jones, B. C., Fink, B., O'Connor, J. J., DeBruine, L. M., Röder, S., & Feinberg, D. R. (2016). Voice parameters predict sex-specific body morphology in men and women. *Animal Behaviour*, 112, 13-22.
- Pi-Sunyer, F. X. (1993). Medical hazards of obesity. *Annals of internal medicine*, 119, 655-660.
- Polak M. (2003). *Developmental Instability: Causes and Consequences*. New York: Oxford Univ. Press
- Pound N, Lawson DW, Toma AM, Richmond S, Zhurov AI, Ian S, Penton-Voak IS. (2014). Facial fluctuating asymmetry is not associated with childhood ill-health in a large British cohort study. *Proc. R. Soc. B* 281, 20141639.
- Pound, N., Penton-Voak, I. S., SurrIDGE, A. K. (2009). Testosterone responses to competition in men are related to facial masculinity. *Proceedings of the Royal Society B*, 276, 153 – 159.

-
- Prentice, A. M., & Jebb, S. A. (2001). Beyond body mass index. *Obesity reviews*, 2(3), 141-147.
- Puhl, R. M., & Latner, J. D. (2007). Stigma, obesity, and the health of the nation's children. *Psychological bulletin*, 133(4), 557.
- Puts, D. A., Gaulin, S. J., & Verdolini, K. (2006). Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and Human Behavior*, 27(4), 283-296.
- Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31(3), 157–175.
- Puts, D. A., Apicella, C. L., & Cárdenas, R. A. (2012). Masculine voices signal men's threat potential in forager and industrial societies. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20110829.
- Puts, D. A., Jones, B. C., & DeBruine, L. M. (2012). Sexual selection on human faces and voices. *Journal of Sex Research*, 49(2-3), 227–243.
- Puts, D. A., Bailey, D. H., Cárdenas, R. A., Burriss, R. P., Welling, L. L., Wheatley, J. R., & Dawood, K. (2013). Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Hormones and Behavior*, 63, 13-19.
- Putignano, P., Dubini, A., Toja, P., Invitti, C., Bonfanti, S., Redaelli, G., ... & Cavagnini, F. (2001). Salivary cortisol measurement in normal-weight, obese and anorexic women: comparison with plasma cortisol. *European Journal of Endocrinology*, 145(2), 165-171.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- 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.
- Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., Kivleniece, I. & Krams, I. (2013a). Facial attractiveness is related to women's cortisol and body fat, but not with immune responsiveness. *Biology Letters*, 9, 20130255.
- Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., ... & Krams, I. (2013b). Adiposity, compared with masculinity, serves as a more

-
- valid cue to immunocompetence in human mate choice. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1751), 20122495.
- Rashad, I. (2008). Height, health, and income in the US, 1984–2005. *Economics & Human Biology*, 6, 108–126.
- Re, D. E., Whitehead, R. D., Xiao, D., & Perrett, D. I. (2011). Oxygenated-blood colour change thresholds for perceived facial redness, health, and attractiveness. *PLoS One*, 6(3), e17859.
- Re, D. E., & Perrett, D. I. (2012). Concordant preferences for actual height and facial cues to height. *Personality and Individual Differences*, 53(7), 901-906.
- Re, D. E., Dzhelyova, M., Holzleitner, I. J., Tigue, C. C., Feinberg, D. R., & Perrett, D. I. (2012). Apparent height and body mass index influence perceived leadership ability in three-dimensional faces. *Perception*, 41(12), 1477-1485.
- Re, D. E., Hunter, D. W., Coetsee, V., Tiddeman, B. P., Xiao, D., DeBruine, L. M., ... & Perrett, D. I. (2013). Looking like a leader—facial shape predicts perceived height and leadership ability. *PloS one*, 8(12), e80957.
- Re, D. E., DeBruine, L. M., Jones, B. C., & Perrett, D. I. (2013). Facial cues to perceived height influence leadership choices in simulated war and peace contexts. *Evolutionary Psychology*, 11, 89-103.
- Re, D. E., Tskhay, K. O., Tong, M. O., Wilson, J. P., Zhong, C. B., & Rule, N. O. (2015). Facing fate: Estimates of longevity from facial appearance and their underlying cues. *Archives of Scientific Psychology*, 3(1), 30.
- Reichlin, S. (1993). Neuroendocrine-immune interactions. *New England Journal of Medicine*, 329(17), 1246-1253.
- 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.
- Rezlescu, C., Penton, T., Walsh, V., Tsujimura, H., Scott, S. K., & Banissy, M. J. (2015). Dominant Voices and Attractive Faces: The Contribution of Visual and Auditory Information to Integrated Person Impressions. *Journal of Nonverbal Behavior*, 39, 355-370.
- Rhodes, G., Proffitt, F., Grady, J. M., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin & Review*, 5(4), 659-669.

-
- Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health?. *Evolution and Human Behavior*, 22(1), 31-46.
- Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health?. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(Suppl 1), 93-95.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annu. Rev. Psychol.* 57, 199-226.
- Rhodes, G., Yoshikawa, S., Palermo, R., Simmons, L. W., Peters, M., Lee, K., Halberstadt, J. & Crawford, J. R. (2007). Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. *Perception* 36, 1244–1252.
- Ritz, B. W., & Gardner, E. M. (2006). Malnutrition and energy restriction differentially affect viral immunity. *The Journal of nutrition*, 136(5), 1141-1144.
- Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., ... & Petrie, M. (2004). Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(Suppl 5), S270-S272.
- Roberts, S.C., Little, A.C., Gosling, L.M., Jone, B.C., Perrett, D.I., Carter, V., and Petrie, M. (2005a) MHC-assortative facial preferences in humans. *Biology Letters*, 1(4), pp. 400-403.
- Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Carter, V., Jones, B. C., Penton-Voak, I., & Petrie, M. (2005b). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, 26, 213–226.
- Roberts, S. C. & Little, A. C. (2007). Good genes, complementary genes and human mate preferences. *Genetica*. 132, 309-321.
- Robins, A. H. (1991). *Biological Perspectives on Human Pigmentation*. Cambridge: Cambridge University Press.
- Roney, J. R., Hanson, K. N., Durante, K. M., Maestriperi, D. (2006). Reading men's faces: women's mate attractiveness judgments track men's testosterone and interest in infants. *Proceedings of the Royal Society B*, 273, 2169 – 2175.

-
- Said, C. P., & Todorov, A. (2011). A statistical model of facial attractiveness. *Psychological Science, 22*, 1183-90.
- Sallmén, M., Sandler, D. P., Hoppin, J. A., Blair, A., & Baird, D. D. (2006). Reduced fertility among overweight and obese men. *Epidemiology, 17*(5), 520-523.
- Samson, N., Fink, B., & Matts, P. (2011). Does a woman's skin color indicate her fertility level?. *Swiss Journal of Psychology*.
- 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*(1), 55-89.
- Schneider, T. M., Hecht, H., & Carbon, C. C. (2012). Judging body weight from faces: The height—weight illusion. *Perception, 41*(1), 121-124.
- Schneider, T. M., Hecht, H., Stevanov, J., & Carbon, C. C. (2013). Cross-ethnic assessment of body weight and height on the basis of faces. *Personality and Individual Differences, 55*(4), 356-360.
- Scott, I. M. L., Pound, N., Stephen, I. D., Clark, A. P., & Penton-Voak, I. S. (2010). Does masculinity matter? The contribution of masculine face shape to male attractiveness in humans. *PLoS ONE, 5*, e13585.
- Scott, I. M., Clark, A. P., Boothroyd, L. G., & Penton-Voak, I. S. (2013). Do men's faces really signal heritable immunocompetence?. *Behavioral Ecology, 24* (3): 579-589.
- 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.
- Seifter, E., Rettura, G., & Levenson, S. M. (1981). *Carotenoids and cell mediated immune responses*. In G. Charamblois & G. Inglett (Eds.), *The Quality of Foods and Beverages: Chemistry and Technology*. New York: Academic Press.
- Sell, A. (2005). Regulating welfare tradeoff ratios: three tests of an evolutionary-computational model of human anger. Doctoral dissertation, University of California Santa Barbara.
- 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.
- Sell, A., Bryant, G. A., Cosmides, L., Tooby, J., Sznycer, D., Von Rueden, C., Krauss, A., & Gurven, M. (2010). Adaptations in humans for assessing physical strength from the voice. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 3509-3518.
- Service, R. F. (1998). New role for estrogen in cancer? *Science*, 279, 1631-1633.
- 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(1599), 2395-2400.
- 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.
- Shackelford, T. K., & Larsen, R. J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of personality and social psychology*, 72(2), 456.
- Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and physical health. *Evolution & Human Behavior*, 20, 71-76.
- Sheldon, B. C. (1994). Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proc. R. Soc. B* 257, 25-30.
- Shepperd, J. A., & Strathman, A. J. (1989). Attractiveness and height – The role of stature in dating preference, frequency of dating, and perceptions of attractiveness. *Personality and Social Psychology Bulletin*, 15, 617-627.
- Simmons, L. W., Rhodes, G., Peters, M., & Koehler, N. (2004). Are human preferences for facial symmetry focused on signals of developmental instability?. *Behavioral Ecology*, 15(5), 864-871.
- Skrinda, I., Krama, T., Kecko, S., Moore, F. R., Kaasik, A., Meija, L., ... & Krams, I. (2014). Body height, immunity, facial and vocal attractiveness in young men. *Naturwissenschaften*, 101(12), 1017-1025.
- Smith, H. M., Dunn, A. K., Baguley, T., & Stacey, P. C. (2016). Concordant cues in faces and voices testing the backup signal hypothesis. *Evolutionary Psychology*, 14, 1-10.

-
- Smith, D. R., & Patterson, R. D. (2005). The interaction of glottal-pulse rate and vocal-tract length in judgements of speaker size, sex, and age a. *The Journal of the Acoustical Society of America*, *118*(5), 3177-3186.
- Sobrinho, A., Mata, M., Laguna-Fernandez, A., Novella, S., Oviedo, P. J., García-Pérez, M. A., ... & Hermenegildo, C. (2009). Estradiol stimulates vasodilatory and metabolic pathways in cultured human endothelial cells. *PloS one*, *4*(12), e8242.
- Sorokowski, P. (2010). Politicians' estimated height as an indicator of their popularity. *European Journal of Social Psychology*, *40*, 1302–1309.
- Stahl, W., Heinrich, U., Jungmann, H., Sies, H., & Tronnier, H. (2000). Carotenoids and carotenoids plus vitamin E protect against ultraviolet light-induced erythema in humans. *American Journal of Clinical Nutrition*, *71*, 795-798.
- 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.
- Steckel, R. H. (1983). Height and per capita income. *Historical Methods*, *16*, 1–7.
- Steiger, J. H. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, *87*, 245.
- Stephen, I. D. (2009). Skin colour, pigmentation and the perceived health of human faces. PhD dissertation. University of St Andrews.
- Stephen, I. D., Smith, M. J. L., Stirrat, M. R., & Perrett, D. I. (2009a). Facial skin coloration affects perceived health of human faces. *International journal of primatology*, *30*(6), 845-857.
- Stephen, I. D., Coetzee, V., Smith, M. L., & Perrett, D. I. (2009b). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS One*, *4*, e5083.
- Stephen, I. D., Coetzee, V., & Perrett, D. I. (2011). Carotenoid and melanin pigment coloration affect perceived human health. *Evolution and Human Behavior*, *32*(3), 216-227.
- 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*(3), 147470491201000312.
- Stephen, I. D., Scott, I. M., 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.
- Stommel, M., & Schoenborn, C. A. (2010). Variations in BMI and prevalence of health risks in diverse racial and ethnic populations. *Obesity*, 18(9), 1821-1826.
- Suri, A., Walters, J. J., Kanagawa, O., Gross, M. L., & Unanue, E. R. (2003). Specificity of peptide selection by antigen-presenting cells homozygous or heterozygous for expression of class II MHC molecules: the lack of competition. *Proceedings of the National Academy of Sciences*, 100(9), 5330-5335.
- Swaddle, J. P., & Reiersen, G. W. (2002). Testosterone increases perceived dominance but not attractiveness in human males. *Proceedings of the Royal Society of London B: Biological Sciences*, 269(1507), 2285-2289.
- Swami, V., Furnham, A., Balakumar, N., Williams, C., Canaway, K., & Stanistreet, D. (2008). Factors influencing preferences for height: A replication and extension. *Personality and Individual Differences*, 45, 395-400.
- Tafeit, E., Möller, R., Pieber, T. R., Sudi, K., & Reibnegger, G. (2000). Differences of subcutaneous adipose tissue topography in type-2 diabetic (NIDDM) women and healthy controls. *American journal of physical anthropology*, 113(3), 381-388.
- 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.
- Tan, K. W., Graf, B. A., Mitra, R. S., & Stephen, I. D. (2017). Impact of fresh fruit smoothie consumption on apparent health of Asian faces. *Evolution & Human Behavior*, in press.
<http://doi.org/10.1016/j.evolhumbehav.2017.02.004>
- Tanner, J. M. (1990). *Foetus into man: Physical growth from conception to maturity*. Harvard University Press.
- Taylor, C. R., Stern, R. S., Leyden, J. J., & Gilchrest, B. A. (1990). Photoaging, photodamage and photoprotection. *Journal of the American Academy of Dermatology*, 22, 1-15.
- Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: averageness, symmetry, and parasite resistance. *Hum. Nat.* 4, 237-269.

-
- Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews of the Cambridge Philosophical Society*, 72(04), 497-548.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in cognitive sciences*, 3(12), 452-460.
- 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.
- 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.
- Tinlin, R. M., Watkins, C. D., Welling, L. L., DeBruine, L. M., Al-Dujaili, E. A., & Jones, B. C. (2013). Perceived facial adiposity conveys information about women's health. *British Journal of Psychology*, 104(2), 235-248.
- Tomkins, J. L., & Simmons, L. W. (2003). Fluctuating asymmetry and sexual selection: paradigm shifts, publication bias, and observer expectation. *Developmental instability: Causes and consequences*, 231-261. New York: Oxford Univ. Press
- Tomkinson, G. R., & Olds, T. S. (2000). Physiological correlates of bilateral symmetry in humans. *International journal of sports medicine*, 21(08), 545-550.
- Torrance, J. S., Wincenciak, J., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2014). The relative contributions of facial shape and surface information to perceptions of attractiveness and dominance. *PloS ONE*, 9, e104415.
- Toscano, H., Schubert, T. W., & Sell, A. N. (2014). Judgments of dominance from the face track physical strength. *Evolutionary Psychology*, 12(1), 147470491401200101.
- Trussell, J. (2004). Contraceptive failure in the United States. *Contraception*, 70(2), 89-96.
- Tybur, J. M. & Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society of London B*, 366, 3375-88.

-
- United Nations Development Programme. (1998). *Human development report* New York, NY: Oxford University Press.
- Urbanek, M. G., Picken, E. B., Kalliainen, L. K., & Kuzon Jr, W. M. (2001). Specific force deficit in skeletal muscles of old rats is partially explained by the existence of denervated muscle fibers. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, 56(5), B191-B197.
- Van Dommelen, W. A., & Moxness, B. H. (1995). Acoustic parameters in speaker height and weight identification: sex-specific behaviour. *Language and speech*, 38(3), 267-287.
- Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. *European Journal of Orthodontics*, 21, 137–143.
- Von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D. & Wittzell, H. (1999). Good genes, oxidative stress and condition-dependent sexual signals. *Proc. R. Soc. B* 266, 1–12.
- 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.
- Waite, C., & Little, A. C. (2006). Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. *International Journal of Primatology*, 27(1), 133-145.
- Wheatley, J. R., Apicella, C. A., Burriss, R. P., Cárdenas, R. A., Bailey, D. H., Welling, L. L., & Puts, D. A. (2014). Women's faces and voices are cues to reproductive potential in industrial and forager societies. *Evolution and Human Behavior*, 35(4), 264-271.
- 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(3), e32988.
- Whitehead, R. D. (2012b). Cross-cultural effects of fruit and vegetable consumption on skin color. *American journal of public health*, 102(2), 212.
- Whitehouse, A. J., Gilani, S. Z., Shafait, F., Mian, A., Tan, D. W., Maybery, M. T., ... & Eastwood, P. (2015). Prenatal testosterone exposure is related to sexually dimorphic facial morphology in adulthood. *Proceedings of the Royal Society B*, 282, 20151351.

-
- WHO, 2000. *Obesity: Preventing and managing the global epidemic*. WHO Technical Report Series 894 (Geneva: WHO), page 9
- Wilson, P. W., D'agostino, R. B., Sullivan, L., Parise, H., & Kannel, W. B. (2002). Overweight and obesity as determinants of cardiovascular risk: the Framingham experience. *Archives of internal medicine*, 162(16), 1867-1872.
- Wincenciak, J., Fincher, C. L., Fisher, C. I., Hahn, A. C., Jones, B. C., & DeBruine, L. M. (2015). Mate choice, mate preference, and biological markets: the relationship between partner choice and health preference is modulated by women's own attractiveness. *Evolution and Human Behavior*, 36(4), 274-278.
- Windhager, S., Schaefer, K., & Fink, B. (2011). Geometric morphometrics of male facial shape in relation to physical strength and perceived attractiveness, dominance, and masculinity. *American Journal of Human Biology*, 23(6), 805-814.
- Windhager, S., Patocka, K., & Schaefer, K. (2013). Body fat and facial shape are correlated in female adolescents. *American Journal of Human Biology*, 25(6), 847-850.
- Wolfe, R. R. (2006). The underappreciated role of muscle in health and disease. *The American journal of clinical nutrition*, 84(3), 475-482.
- Wolffhechel, K., Hahn, A. C., Jarmer, H., Fisher, C. I., Jones, B. C., & DeBruine, L. M. (2015). Testing the utility of a data-driven approach for assessing BMI from face images. *PloS one*, 10(10), e0140347.
- Xie, Q., & Zhang, M. (2013). White or tan? A cross-cultural analysis of skin beauty advertisements between China and the United States. *Asian Journal of Communication*, 23(5), 538-554.
- Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of theoretical Biology*, 53_, 205-214.
- Zahavi, A. and Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. New York: Oxford University Press.
- 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, 167-185.