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Healthy body, healthy face? Evolutionary approaches to attractiveness perception

The human face contains a large amount of observable information about the bearer, providing cues to age, sex, ethnic group and emotional state. Observers also make spontaneous judgements about more apparently subjective attributes, such as how attractive they consider the face to be. Recent developments in evolutionary psychology suggest that these perceptions of attractiveness may not be so subjective after all, and may in fact reflect aspects of the underlying health and fertility of the bearer. In order for a cue to health to be valid, however, it must both relate to the actual health of the bearer *and* be perceived as healthy and/or attractive by observers (Coetzee, Perrett & Stephen, 2009; Fig. 1). In this chapter, we will introduce the theoretical approaches to attractiveness research, and discuss the evidence for health cues in the face and agreement and variation in face preferences.

Theoretical approaches to attractiveness research

Most people will have heard the proverb "beauty is in the eye of the beholder", which implies that attractiveness is somewhat arbitrary and subjective. This opinion was adopted by Darwin in his *Descent of Man*, where he writes "the men of each race prefer what they are accustomed to" (Darwin, 1871), implying that preferences are learned from the social environment, and imprinted on those faces we see around us during development. In the 20th century, feminist thinkers adopted this theme, with Naomi Wolf suggesting in *The Beauty Myth* that female beauty was arbitrary, socially constructed and culturally imposed by the patriarchy as a method of maintaining control over women (Wolf, 1991). In this framework, concepts of beauty are predicted to vary substantially and arbitrarily across individuals and across cultures. However, studies have repeatedly shown that, while small variations in face preferences are seen between individuals and between cultures, there is a high degree of agreement on what makes a face attractive and a mate desirable (Buss, 1989; Langlois et al, 2000), calling the social construct hypothesis into doubt.

Buss (1989) conducted a large scale survey of 37 diverse cultures from around the world, finding that women rated cues to ability and willingness to invest in her and her offspring (such as ambition and good financial prospects) as important in a husband. Men, on the other hand, prioritised cues to youth and fertility in women (Buss & Schmitt, 1993; Townsend, & Wasserman, 1998; Li, Valentine & Patel, 2010). There is also considerable agreement across cultures on what makes a face look attractive. Similar preferences have been found for symmetrical faces in cultures as diverse as Australian, Japanese (Rhodes et al, 2001), Scottish (Perrett et al, 1998), Hadza (an African hunter-gatherer society; Little et al, 2007), and even in Rhesus macaque monkeys (Waitt & Little, 2006). Preferences for faces close to the population average shape (Rhodes et al, 2001), as well as for slightly redder, yellower and lighter skin colour (Stephen et al, 2009a; 2012; Stephen, Coetzee & Perrett, 2011; Scott et al, 2010) and for more feminine female faces (Perrett et al, 1998) have all been found cross-culturally as well. While some variation in preferences does exist between cultures (DeBruine et al, 2010; Marlowe, Apicella & Reed, 2005; Tovee et al, 2006), it is important to ask why these traits are considered desirable in diverse cultures.

Researchers have begun to use evolutionary theory to explain attractiveness as a mate selection mechanism (Lee et al., 2008), allowing people to identify and attract healthy mates with whom to reproduce (Thornhill & Gangestad, 1999). Mate selection is of critical importance in sexually reproducing species, since it determines the levels of direct and indirect benefits that will accrue to offspring. Direct benefits include nuptial gifts, such as meat provided by men to women in exchange for sexual access in many traditional societies (Wood & Hill, 2000) and parental care of offspring, whereas indirect benefit refers to the genes that are passed on to the offspring (Trivers, 1972). Since healthy mates represent a lower risk of infection during courtship and mating, and are likely to be able to provide higher quality investment and better genes to the offspring, it is clear that choosing a healthy mate is an important ability. Those individuals who are able to identify and choose healthier mates will leave more healthy offspring; and genes for identifying and choosing healthy mates will increase in frequency in the population (Trivers, 1972). Similarly, those individuals who are best able to advertise their health and attract high quality mates will leave more healthy offspring, and thus their genes will increase in frequency in the population. This process is known as sexual selection (Darwin, 1871).

In most animal species, the female invests more in the offspring than does the male. For female mammals, the minimum investment required to produce a healthy offspring involves investing considerable time and energy in gestation, breastfeeding and in many species prolonged periods of infant dependence upon the mother for protection and food. For males, on the other hand, the minimum investment in a healthy offspring is a small amount of time and energy invested in the act of mating itself (Trivers, 1972). Further, female mammals are limited by biology in the number of offspring they can produce, whereas males can potentially produce a much larger number of offspring, primarily limited by access to females (Bateman, 1948). For this reason, in most species, females tend to be choosier than males, whereas males compete for access to females, for example by fighting (for example in the elephant seal; LeBouef, 1974) or by exhibiting large, brightly coloured ornaments (for example in the goldfinch; Saks, Ots & Horak, 2003). However, in species where male investment is substantial, such as humans, evolutionary theory predicts that males will also be choosy, at least when looking for a long term mate (Trivers, 1972).

What defines attractiveness?

In recent decades, researchers have begun to identify the facial cues that affect attractiveness, with studies showing effects of symmetry (Gangestad, Thornhill & Yeo, 1994; Grammer & Thornhill, 1994;

Mealey, Bridgstock & Townsend, 1999; Penton-Voak *et al.*, 2001; Perrett *et al.*, 1999), averageness (Langlois & Roggman, 1990; Langlois, Roggman & Musselman, 1994; Rhodes, Sumich & Byatt, 1999), masculinity or femininity (also known as sexual dimorphism; Perrett *et al.*, 1998; Rhodes *et al.*, 2003; Rhodes *et al.*, 2007) and skin colour (Stephen et al, 2012; Scott et al, 2010). Many of these studies have suggested that these aspects of facial appearance are perceived as attractive because they represent valid cues to health. However, in order for a trait to be a valid cue to health, it must be shown to relate both to perceived health and/or attractiveness *and* to an aspect of underlying health (Fig 1; Coetzee et al, 2009). While relationships have been found between many facial traits and apparent health/attractiveness, studies connecting these traits to aspects of real, underlying health are less abundant (Coetzee et al, 2009).

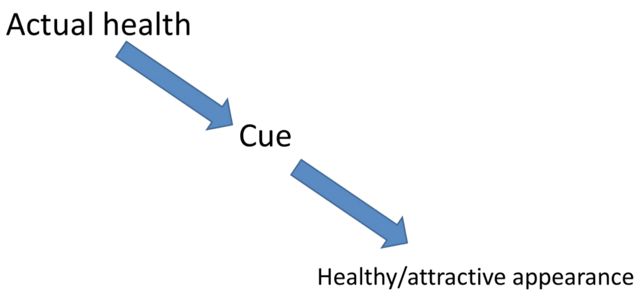

Figure 1: In order for a facial trait to be considered a valid cue to health, it must relate to both an aspect of actual health *and* healthy and/or attractive appearance.

Evidence connecting perceived health to actual health

Face shape

Symmetry is perceived as attractive by humans in diverse cultures (Gangestad *et al.*, 1994; Grammer & Thornhill, 1994; Mealey *et al.*, 1999; Penton-Voak *et al.*, 2001; Perrett *et al.*, 1999), and is preferred in mates by non-human animals such as macaques (Waitt & Little, 2006), barn swallows (Møller, 1994) and zebra finches (Swaddle & Cuthill, 1994). This fulfils one half of the requirement for a valid cue to health (fig 1), but a connection from symmetry to actual health is also required (Coetzee et al, 2009). Under this hypothesis, it has been proposed that symmetry is an indicator of the health of the individual during development (see Perrett et al, 1999). Our genes provide a "blueprint" for how to build a fully grown adult and, in ideal conditions, this fully grown adult would be symmetrical. However, ideal conditions are hard to find in the real world, and a variety of occurrences will interfere with optimal development, such as infectious diseases and illnesses, malnutrition or poor diet. It is proposed that the fluctuating asymmetry (small deviations from perfect symmetry in the face and body) of a face reflects the bearer's *developmental stability*, and therefore is a good indicator of how often and how severely the individual's development was interrupted, and also how well that individual was able to resist the interruption – for example how well his immune system was able to fight off the infection (Møller, 1990).

A number of studies have attempted to relate facial symmetry to measures of actual health, including developmental (childhood) health. Shackelford & Larsen (1997) collected a wide range of mental and physical health measures by questionnaires, and measured symmetry from photographs of 101 students in Michigan, USA, in order to see if symmetry correlated with health. They found 54 relationships between the psychological health measures and the symmetry of the participants. However, Perrett (2010) points out that, with so many comparisons (918 in all), we would expect to find almost this many significant relationships through chance alone, so this study does not provide the evidence we need. Rhodes et al (2001) attempted to provide a more reliable link between developmental health and facial symmetry in a sample of 316 adolescents. They used medical records from childhood and adolescence (and gave each individual health scores based on these records), and symmetry measured from photographs. While they found evidence of a link between symmetry and attractiveness, they found no relationship between the developmental health and symmetry measures. Most recently, Pound et al. (2014) used a large sample of 4000 individuals from the ALSPAC database in Avon, UK. Symmetry was measured from 3D laser scans and health measures were made at intervals during childhood. They found no lasting effect of childhood illnesses on symmetry, but did find that illness made children temporarily less symmetrical. They also found that children from wealthier backgrounds had more symmetrical faces. So it may be that symmetry is a better indicator of the childhood and adolescent nutrition aspects of developmental stability than it is of childhood and adolescent illness.

Averageness is another cue that has been found to appear healthy and attractive. It is possible to make average blends of faces using computer technology. This involves marking many points on each face photograph, such as the corners of the eyes and mouth, and giving each point a set of coordinates. By taking the average location of each point across your whole set of face photographs, you can make a face of average shape. By then averaging the colour of each pixel across the faces, you make your average shaped face have average colour too (Tiddeman, Stirrat & Perrett, 2005). Langlois & Roggmann (1990) found that these average faces are more attractive than the individual faces from which they are made. Rhodes et al (2001) found that this effect is found cross-culturally by testing in Japan. It was suggested that the reason these faces looked attractive is participants were avoiding distinctive faces, which might suggest that they are suffering from some kind of illness or that they are carrying unhealthy genes (Rhodes & Tremewan, 1996), whereas individuals who have average faces may have more heterozygosity in the area of DNA known as the major histocompatibility complex (MHC). This means that they have more varied genes for immune function and can therefore produce the necessary immune proteins to fight off a broader range of pathogens (Thornhill & Gangestad, 1993). It has since been found that people with very distinctive faces *do* suffer from more illnesses than average-looking people (Zebrowitz & Rhodes, 2004; Rhodes et al, 2001), and that people with more heterozygosity in the MHC are perceived as looking (Roberts et al, 2005) and even smelling (Thornhill et al, 2003) more attractive. Interestingly, it was recently found that people who are very sensitive to feeling disgusted when they see something that carries a risk of infection (e.g. vomit, faeces, and rotten food) find unattractive faces even less attractive than other people do. This suggests that these hypersensitive people might be trying to avoid any chance of infection by avoiding unattractive people who might be more susceptible to illness (Park, van Leeuwen & Stephen, 2012).

Body shape

Body weight is also an important determinant of attractiveness. It has been found that, in developed societies, men typically find women in the middle of the healthy body mass index range (BMI; 19–24.5 for Caucasian populations) look the healthiest, whereas women at the lower end of the healthy range look the most attractive (Tovee et al, 1998, Tovee & Cornelissen, 1999; Thornhill & Grammer, 1999; Swami & Tovee, 2005; Stephen & Perera, 2014a, b). This weight is also visible in the face (Coetzee et al, 2009), and facial adiposity (apparent weight in the face) consistent with the same body weight also looks healthiest and most attractive (Coetzee et al, 2011). The connection between body weight and health is also very well known, with overweight and obese individuals at increased risk of a range of illnesses including diabetes, coronary illnesses, stroke and various cancers (Wilson et al, 2002). Underweight individuals have reduced immune function, energy levels and are more prone to infection (Ritz & Gardner, 2006). Both overweight and underweight women are also at increased risk of infertility (Green, Weiss & Daling, 1988). Increased facial adiposity has also been associated with risk factors such as increased blood pressure, increased susceptibility to infections (Coetzee et al, 2009) and decreased progesterone levels (Tinlin et al, 2012). Interestingly, in parts of the world where food security is less reliable, and heavier body weight thus represents an ability to find sufficient food, such as sub-Saharan Africa (Tovee et al, 2006) and rural parts of Malaysia (Swami & Tovee, 2005), preferences shift towards higher body weight, suggesting that preferences respond to ecological and social environmental conditions in a way that is consistent with evolutionary theory. So, it seems like body weight and facial adiposity may represent valid cues to health.

Sexual dimorphism

Sexual dimorphism can be thought of as masculinity or femininity. That is, how typically male or typically female a person is. Sex-typical characteristics of the face and body develop under the influence of sex hormones. In males, testosterone drives increased muscle mass, taller stature, increased body hair, jaw, nose and brow ridge growth (see Penton-Voak & Chen, 2004), while in females, oestrogen drives the development of breasts, buttocks and lips, and inhibition of body hair, nose, jaw and brow ridge growth. Oestrogen in women is associated with increased fecundity, with women with higher levels of oestrogen being more likely to conceive (Stewart et al, 1993; Lipson & Ellison, 1996; Baird et al, 1997, 1999). Perrett et al (1998), transformed Caucasian and Japanese women's faces to make them more typically female (feminised) or more typically male (masculinised), and asked Caucasian and Japanese participants to indicate the most attractive level of feminisation or masculinisation. Participants chose faces that were feminised, regardless of ethnicity. Law Smith et al (2006) found that women's oestrogen levels predict ratings of femininity, attractiveness and health, making femininity a valid cue to women's reproductive health.

Men's masculinity, similarly, has been suggested to be a valid cue to men's health, reflecting increased testosterone levels. Since testosterone is thought to suppress the immune system, men who can maintain high levels of testosterone during development, in order to produce a masculine face shape, and still be able to fight off infection, must be of high quality and have good genes (Hamilton & Zuk, 1982; Zahavi, 1975). This is known as the Immunocompetence Handicap Hypothesis (Hamilton & Zuk, 1982). It was therefore predicted that masculine men would be considered more attractive. However, Perrett et al (1998) found that women preferred more *feminine* male faces. It was suggested that the negative personality traits, such as aggression and infidelity, attributed to masculine men may limit the attractiveness of masculine facial appearance (Perrett et al, 1998; Mazur & Booth, 1998). More recent research has shown that women's preferences for masculinity in men's faces changes in response to the social environment, as well as to changes in women's fertility and own attractiveness. It has been suggested that women should prefer more feminine men, who would make a better partner and father, for a long term partner, and prefer more masculine men, who carry "good genes" during the fertile phase of the menstrual cycle. This would allow her to obtain good genes for her offspring from a masculine man, while securing the parental investment of a feminine man. Indeed, this has been confirmed, as women's preferences shift to prefer more masculine men during the fertile phase of the menstrual cycle (Penton-Voak et al, 1999; Penton-Voak & Perrett, 2000) and when seeking short term relationships (Little et al, 2002). Cross-cultural factors also cause changes in women's preferences for men's masculinity, with women who live in countries with high levels of income inequality, competition and parasites preferring more masculine men, who are perhaps better able to compete in such environments, than women who live in less unequal, competitive and parasite-laden environments (Brooks et al, 2011; DeBruine et al, 2010). So the picture for masculinity preferences reflects trade-offs in the reproductive and health benefits that can be provided by masculine and feminine men, whereby masculine men offer good genes and feminine men offer parental investment. Women's preferences changing according to social and ecological environment and own fertility, in line with the predictions of evolutionary theory.

Skin colour and texture

The skin itself may also hold cues to the health of individuals. Jones et al (2004) cropped squares of skin from photographs of people's faces, and asked participants to rate how healthy the skin looked. People whose skin was rated as looking healthier were also rated as more attractive from photographs of their whole face, suggesting that having healthy looking skin is an important aspect of attractiveness. It has since been shown that both skin colour distribution (Fink, Grammer & Matts, 2006; Fink et al, 2012; Matts et al., 2007) and overall skin colour (Scott et al, 2010; Stephen et al, 2009a, 2009b, 2011, 2012) play an important role in the attractive and healthy appearance of faces. Skin with a smoother, more even colour distribution appears younger, healthier and more attractive in both women's (Matts et al., 2007) and men's (Fink et al., 2012) faces. This colour distribution relates to actual health in that exposure to damaging UV light, as well as ageing, cause pigments to become less evenly distributed throughout the skin (Matts & Fink, 2010). The attractiveness of an even skin colour distribution therefore reflects less skin damage and degradation.

Overall skin colour also affects the healthy and attractive appearance of faces. Participants were asked to use a computer programme to manipulate the colour of skin portions of colour calibrated face photographs to make them appear as healthy as possible. Participants chose to increase the redness, yellowness and lightness of the skin (Stephen et al, 2009a). Skin redness is primarily determined by the amount of blood and the oxygenation state of the haemoglobin (the red pigment in blood that transports oxygen around the body) in the blood. Since increased blood perfusion and oxygenation are associated with physical fitness (Armstrong & Welsman, 2001; Johnson, 1998), increased oestrogen (a female sex hormone) in women (Charkoudian et al, 1999) and the absence of certain respiratory and cardiac diseases (Panza et al, 1990), the researchers suggested that this preference for red skin may represent a valid cue to health. Indeed, further studies showed that increased *oxygenated* blood colour in particular enhances the apparent health of faces (Stephen et al, 2009b).

The yellow colour of the skin is primarily influenced by melanin (the dark brown pigment associated with sun tanning; Stamatas et al, 2004) and carotenoids (Alaluf et al, 2002). Melanin protects the skin from the damaging effects of ultraviolet light, and from sunburn and cancer (Robins, 1991), but can prevent the formation of vitamin D, potentially leading to osteomalacia and rickets (weak, deformed bones; Murray, 1934). Carotenoids are antioxidant pigments that we get from fruit and vegetables in our diet (Alaluf et al, 2002). Carotenoids protect the body from the damaging effects of reactive oxygen species (ROS). These ROS are chemicals formed in the body by metabolic processes, especially due to immune functioning and the reproductive system, and they can damage cell structures including proteins and DNA if they are not neutralised by antioxidants, such as carotenoids (Dowling & Simmons, 2009). Indeed, reduced carotenoid levels have been associated with infectious diseases such as HIV and malaria (Friis et al, 2001). Stephen et al, 2011, found that the preference for yellow skin is explained by a much stronger preference for the particular hue of yellow caused by increased levels of carotenoids in the skin than by the yellow-brown colour of melanin. Further, they found that individuals who eat a healthy diet with higher levels of fruit and vegetables have yellower skin (Stephen et al, 2011). It therefore seems that skin colour represents a valid cue to health, reflecting carotenoid levels in the diet and, possibly, freedom from infection. Further, it has been shown that humans can detect smaller changes in colour in human facial skin than they can in simple patches of colour, supporting the suggestion that facial skin colour has special salience (Tan & Stephen, 2013). It has even been suggested that primate colour vision evolved to allow us to detect colour-based social information from faces (Changizi et al, 2006)!

Interestingly, these colour cue mechanisms are also found in other animal species. While colour signals are not found in non-primate mammals, who do not have trichromatic vision (what humans would consider to be full colour vision; Carroll et al, 2001), they are found in primates, many species of which do have trichromatic colour vision, and in many bird and fish species, many of which can distinguish more colours than humans. In rhesus macaques (monkeys), male faces become redder in the mating season, in response to increased levels of testosterone (Rhodes et al, 1997). Female macaques show preferential looking behaviour towards redder versions of photographs of male faces (Waitt et al, 2003). Male mandrills (a type of baboon) have a bright red ornamented face, which becomes redder with increased testosterone levels (Setchell & Dixson, 2001). Other males avoid violent conflict with redder faced males (Setchell & Wickings, 2005), and female mandrills prefer to mate with males with redder faces, regardless of dominance rank (Setchell, 2005). Females also use red skin signals to advertise their health and fertility. Female rhesus macaques experience "sexual swellings", with the skin around the genital area becoming redder when the female is in oestrus (fertile). Males pay more attention to, and direct more mating effort towards, redder females (Waitt et al, 2006). Many species of birds and fish also use colourful ornaments to signal health, often based upon carotenoids. For example, the size and brightness of greenfinches' (a bird with a bright yellow feathered ornament) carotenoid based ornament reflects parasite load, with those individuals with bigger and brighter ornaments having fewer parasites (Saks et al, 2003; Horak et al, 2004), and there is evidence that goldfinches select mates based on the size and brightness of carotenoid ornament (MacDougall & Montgomerie, 2003). It seems, therefore, that similar mechanisms may be operating in very different species.

Conclusion

In conclusion, the human face and body provide an array of cues that are interpreted by observers as healthy and/or attractive. While the social construct hypothesis predicts that these preferences are arbitrary, a range of evidence from across psychology, anthropology and animal behaviour suggests that the preferences are predictable by considering their relationship with the underlying health of the bearer. While a number of cues have been identified as appearing healthy and attractive, and some have been confirmed as valid cues to health, such as facial adiposity and skin colour, by relating them to aspects of real health, more research is needed to reliably connect some other cues, such as symmetry or averageness, to real health. Contrary to popular belief, evolutionary theories of attraction do not predict preferences that are unchanging regardless of social and ecological environment, but rather predict flexible preferences that vary according to the environment, in order to allow people to identify appropriate and high quality mates in the prevailing conditions. The literature reviewed here shows considerable cross-cultural agreement in attractiveness preferences, but also shows changing preferences in response to social and environmental factors.

References

Alaluf, S., Heinrich, U., Stahl, W., Tronnier, H., & Wiseman, S. (2002). Dietary carotenoids contribute to normal human skin color and UV photosensitivity. *Journal of Nutrition, 132,* 399–403.

Armstrong N., & Welsman J. R. (2001). Peak oxygen uptake in relation to growth and maturation in 11–17-year-old humans. *European Journal of Applied Physiology, 85,* 546–551.

Baird, D. D., Wilcox, A. J., Weinberg, C. R., Kamel, F., McConnaughey, D. R., Musey, P. I., & Collins, D. C. (1997). Preimplantation hormonal differences between the conception and non-conception menstrual cycles of 32 normal women. *Human Reproduction Update, 12*(12), 2607–2613.

Baird, D. D., Weinberg, C. R., Zhou, H., Kamel, F., McConnaughey, D. R., Kesner, J. S., & Wilcox, A. J. (1999). Preimplantation urinary hormone profiles and the probability of conception in healthy women. *Fertility & Sterility, 71,* 40–49.

Bateman, A. J. (1948). Intra-sexual selection in Drosophila. *Heredity, 2,* 349–368.

Brooks, R., Scott, I. M., Maklakov, A. A., Kasumovic, M. M., Clark, A. P., & Penton-Voak, I. S. (2011). National income inequality predicts women's preferences for masculinised faces better than health does. *Proceedings of the Royal Society of London B. 278,* 810–812.

Buss, D. M. (1989). Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*, 1–49.

Buss, D. M., & Schmidt, D. P. (1993). Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review, 100*, 204–232.

Carroll, J., Murphy, C. J., Neitz, M., ver Hoeve, J. N., & Neitz, J. (2001). Photopigment basis for dichromatic colour vision in the horse. *Journal of Vision, 1*, 80–87.

Changizi, M.A., Zhang, Q., Shimojo, S. (2006) Bare skin, blood and the evolution of primate colour vision. *Biology Letters, 2,* 217–221.

Charkoudian, N., Stephens, D. P., Pirkle, K. C., Kosiba, W. A., & Johnson, J. M. (1999). Influence of female reproductive hormones on local thermal control of skin blood flow. *Journal of Applied Physiology, 87,* 1719–1723.

Coetzee, V., Perrett, D. I., & Stephen, I. D. (2009). Facial adiposity: a cue to health? *Perception, 38,* 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,* 190–193.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & 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, 277*(1692), 2405–2410.

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,* 276, 1737–1745.

Fink, B., Grammer, K., & Matts, P. J. (2006). Visible skin color distribution plays a role in the perception of age, attractiveness, and health in female faces. *Evolution and Human Behavior, 27*, 433–442.

Fink, B., Bunse, L., Matts, P. J., D'Emiliano, D. (2012). Visible skin colouration predicts perception of male facial age, health and attractiveness. *International Journal of Cosmetic Science, 34,* 307–310.

Friis, H., Gomo, E., Kastel, P., Ndhlovu, P., Nyazema, N., Krarup, H., & Michaelsen, K. F. (2001). HIV and other predictors of serum β-carotene and retinol in pregnancy: a cross-sectional study in Zimbabwe. *American Journal of Clinical Nutrition, 73,* 1058–1065.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology, 15*, 73–85.

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

Green, B. B., Weiss, N. S., & Daling, J. R. (1988). Risk of ovulatory infertility in relation to body weight. *Fertility and Sterility, 50,* 721–725.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science, 218*, 384–387.

Horak, P., Saks, L., Karu, U., Ots, I., Surai, P. F., & McGraw, K. J. (2004). How coccidian parasites affect health and appearance of greenfinches. *Journal of Animal Ecology, 73,* 935–947.

Johnson, J. M. (1998). Physical training and the control of skin blood flow. *Medicine and Science in Sports and Exercise, 30*, 382–386.

Jones, B. C., Little, A. C., Burt, D. M., & Perret, D. I. (2004). When facial attractiveness is only skin deep. *Perception, 33*, 569–576.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin, 126*(3), 390–423.

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

Langlois, J. H., Roggman, L. A., & Musselman, L. (1994). What is average and what is not average about attractive faces? *Psychological Science, 5*(4), 214–220.

Law Smith, M. J., Perrett, D. I., Jones, B. C., Cornwell, R. E., Moore, F. R., Feinberg, D. R., Hillier, S. G., (2006). Facial appearance is a cue to oestrogen levels in women. *Proceedings of the Royal Society of London B, 273,* 135–140.

LeBouef, B. L. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist, 14,* 163–176.

Lee, L., Loewenstein, G., Ariely, D., Hong, J., & Young, J. (2008). If I'm not hot, are you hot or not? Physical-attractiveness evaluations and dating preferences as a function of one's own attractiveness. *Psychological Science*, *19*(7), 669–677.

Li, N.P., Valentine, K.A., & Patel, L. (2011). Mate preferences in the U.S. and Singapore: A cross-cultural test of the mate preference priority model. *Personality and Individual Differences, 50*, 291–294.

Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Preferences for symmetry in faces change across the menstrual cycle. *Biological Psychology, 76*, 209–216.

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B: Biological Sciences, 269*, 1095–1100.

Lipson, S. F., & Ellison, P. T. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Human Reproduction, 11*(10), 2090–2096.

MacDougall, A. K., & Montgomerie, R. (2003). Assortative mating by carotenoid-based plumage color: A quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften, 90*, 464–467.

Marlowe, F., Apicella, C., & Reed, D. (2005). Men's preferences for women's profile waist-to-hip ratio in two societies, *Evolutionary Human Behavior*, *26*, 458–468.

Matts, P. J., & Fink, B. (2010). Chronic sun damage and the perception of age, health and attractiveness. *Photochemical and Photobiological Sciences, 9*, 421–431.

Matts, P. J., Fink, B., Grammer, K., & Burquest, M. (2007). Colour homogeneity and visual perception of age, health and attractiveness of female facial skin. *Journal of the American Academy of Dermatology, 57*(6), 977–984.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioural and Brain Sciences, 21*, 353–397.

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

Møller, A. P. (1990). Parasites and sexual selection: Current status of the Hamilton and Zuk hypothesis. *Journal of Evolutionary Biology, 3,* 319–328.

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

Murray, F. G. (1934). Pigmentation, sunlight and nutritional disease. *American Anthropologist, 36*(3), 438–448.

Panza, J. A., Quyyimi, A. A., Brush, J. R., & Epstein, S. E. (1990). Abnormal endothelium-dependent vascular relaxation in patients with essential hypertension. *New England Journal of Medicine, 323*, 22–27.

Park, J. H., van Leeuwen, F., & Stephen, I. D. (2012). Homeliness is in the disgust sensitivity of the beholder: relatively unattractive faces appear especially unattractive to individuals higher in pathogen disgust. *Evolution and Human Behavior, 33,* 569–577.

Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolutionary Human Behavior, 25,* 229–241.

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*, 1617–1623.

Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically. *Evolution and Human Behavior, 21*, 39–48.

Penton-Voak, I. S., Perrett, D., Castles, D., Burt, M., Koyabashi, T., & Murray, L. K. (1999). Female preferences for male faces change cyclically. *Nature, 399*, 741–742.

Perrett, D. (2010). *In Your Face: The New Science of Human Attraction*. New York, NY: Palgrave Macmillan.

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*, 295–307.

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394,* 884–887.

Pound, N., Lawson, D.W., Toma, A.M., Richmond, S., Zhurov, A.I., Penton-Voak, I.S. (2014). Facial fluctuating asymmetry is not associated with childhood ill-health in a large British cohort study. *Proceedings of the Royal Society of London B: Biological Sciences, 281*, 20141639.

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*, S93–S95.

Rhodes, G., Sumich, A., & Byatt, G. (1999). Are Average Facial Configurations Attractive Only Because of Their Symmetry? *Psychological Science, 10*(1), 52–58.

Rhodes, G., & Tremewan, T. (1996). Averageness, exaggeration and facial attractiveness. *Psychological Science, 7,* 105–110.

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

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

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 Behaviour, 22*(1), 31–46.

Rhodes, L., Argersinger, M. E., Gantert L. T., Friscino, B. H., Hom, G., Pikounis, B., Rhodes, W. L. (1997). Effects of administration of testosterone, dihydrotestosterone, oestrogen and fadrozole, an aromatase inhibitor, on sex skin colour in intact male rhesus macaques. *Journal of Reproduction and Fertility, 111,* 51–57.

Ritz, B. W., & Gardner, E. M. (2006). Malnutrition and energy restriction differentially affect viral immunity. *The Journal of Nutrition, 136*, 1141–1144.

Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Jones, B. C., Carter, V., Petrie, M. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution & Human Behavior, 26*, 213–226.

Robins, A. H. (1991). *Biological Perspectives on Human Pigmentation*. Cambridge: Cambridge University Press.

Saks, L., Ots, I., & Horak, P. (2003). Carotenoid-based plumage coloration of male greenfinches reflects health and immunocompetence. *Oecologia*, *134*, 301–307.

Scott, I. M. L., Pound, N., Stephen, I. D., Clark, A. P., & Penton-Voak, I. S. (2010). Does masculinity matter? The contribution of sex-typical appearance to male attractiveness in humans. *PLoS ONE, 5*, e13585.

Setchell, J. M. (2005). Do female mandrills prefer brightly coloured males? *International Journal of Primatology, 26*(4), 715–735.

Setchell, J. M., & Dixson, A. F. (2001). Changes in the Secondary Sexual Adornments of Male Mandrills (Mandrillus sphinx) Are Associated with Gain and Loss of Alpha Status. *Hormones and Behavior, 39*(3), 177–184.

Setchell, J. M., & Wickings, J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology, 111*, 25–50.

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*, 456–466.

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.

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., Coetzee, V., Smith, M. L., & Perret, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS One 4(4)*, e5083.

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

Stephen, I. D., Smith, M. J. L., Stirrat, M. R., & Perrett, P. I. (2009). Facial Skin Coloration Affects Perceived Health of Human Faces. *International Journal of Primatology. 30*(6), 845–857.

Stephen, I.D., & Perera, A.T.M. (2014). Judging the difference between attractiveness and health: Does exposure to model images influence the judgments made by men and women? *PLoS one, 9*, e86302.

Stephen, I.D., & Perera, A.T.M. (2014). Judging the difference between women's attractiveness and health: Is there really a difference between judgments made by men and women? *Body Image, 11*, 183–186.

Stewart, D., Overstreet, J., Nakajima, S., & Lasley, B. (1993). Enhanced ovarian steroid secretion before implantation in early human pregnancy. *Journal of Clinical Endocrinology & Metabolism, 76*(6), 1470–1476.

Swaddle, J. P., & Cuthill, I. C. (1994). Preference for symmetrical males by female zebra finches. *Nature, 367*, 165–166. doi:10.1038/367165a0.

Swami, V. & Tovée, M. J. (2005). Female physical attractiveness in Britain and Malaysia: A cross-cultural study. *Body Image, 2,* 115–128.

Tan, K.W., & Stephen, I.D. (2013). Colour detection thresholds in faces and colour patches. *Perception, 42*, 733–741.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature, 4*, 237–269.

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. *Behavioural Ecology, 14*(5), 668–678.

Thornhill, R., & Grammer, K. (1999). The body and face of a woman: one ornament that signals quality? *Evolution and Human Behaviour, 20*, 105–120.

Tiddeman, B. P., Stirrat, M. R., & Perrett, D. I. (2005). Towards realism in facial transformation: results of a wavelet MRF method. *Computer Graphics Forum, 24*(3), 449–456.

Tinlin, R. M., Watkins, C. D., Welling, L. L. M., DeBruine, L. M., Al-Dujaili, E. A. S., & Jones, B. C. (2012). Perceived facial adiposity conveys information about women's health. *British Journal of Psychology, 104,* 235–348. doi: 10.1111/j.2044-8295.2012.02117.x.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man: 1871–1971* (pp. 136–179). Chicago, IL: Aldine.

Tovée, M. J., & Cornelissen, P. L. (1999). The mystery of female beauty. *Natur*e, 399, 215–216.

Tovée, M. J., Reinhardt, S., Emery, J. L., & Cornelissen, P. L. (1998). Optimum body-mass index and maximum sexual attractiveness. Lancet, *352*(9127), 548–548.

Tovée, M. J., Swami, V., Furnham, A., & Mangalparsad, R. (2006). Changing perceptions of attractiveness as observers are exposed to a different culture. *Evolution and Human* Behavior, *27*(6), 443–456.

Townsend, J. M., & Wasserman, T. (1998). Sexual strategies theory: an evolutionary perspective on human mating. *Evolution and Human Behavior, 19*, 171–191.

Waitt, C., Gerald, M. S., Little, A. C., & Kraiselburd, E. (2006). Selective attention toward female secondary sexual color in male rhesus macaques. *American Journal of Primatology, 68,* 738–744.

Waitt, C., & Little, A. C. (2006). Preferences for symmetry in conspecific facial shape among Macaca mulatta. *International Journal of Primatology, 27*, 133–145.

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

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. *Archive of Internal Medicine, 162,* 1867–1872.

Wolf, N. (1991). *The beauty myth: How images of beauty are used against women.* New York, NY: William Morrow and Company.

Wood, B., & Hill, K. (2000). A test of the "showing-off" hypothesis with Ache hunters. *Current Anthropology, 41,* 124–125.

Zahavi, A. (1975). Mate selection – a selection for a handicap. *Journal of Theoretical Biology, 53*, 205–214.

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.