



Facial attractiveness

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Facial attractiveness has important social consequences. Despite a widespread belief that beauty cannot be defined, in fact, there is considerable agreement across individuals and cultures on what is found attractive. By considering that attraction and mate choice are critical components of evolutionary selection, we can better understand the importance of beauty. There are many traits that are linked to facial attractiveness in humans and each may in some way impart benefits to individuals who act on their preferences. If a trait is reliably associated with some benefit to the perceiver, then we would expect individuals in a population to find that trait attractive. Such an approach has highlighted face traits such as age, health, symmetry, and averageness, which are proposed to be associated with benefits and so associated with facial attractiveness. This view may postulate that some traits will be universally attractive; however, this does not preclude variation. Indeed, it would be surprising if there existed a template of a perfect face that was not affected by experience, environment, context, or the specific needs of an individual. Research on facial attractiveness has documented how various face traits are associated with attractiveness and various factors that impact on an individual's judgments of facial attractiveness. Overall, facial attractiveness is complex, both in the number of traits that determine attraction and in the large number of factors that can alter attraction to particular faces. A fuller understanding of facial beauty will come with an understanding of how these various factors interact with each other. © 2014 John Wiley & Sons, Ltd.

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INTRODUCTION

The human face has been a source of great interest to psychologists and other scientists because of the extraordinarily well-developed ability of humans to process, recognize, and draw information from others' faces.¹ Faces dominate our works of art, ancient and modern, and our sensitivity to faces is highlighted when we see faces in many everyday shapes under ambiguous conditions, such as in clouds or the face of the man in the moon. Human infants only minutes old attend particularly to face like stimuli compared with equally complicated non-face stimuli.^{2,3} One aspect of faces that appears to have a powerful hold over our lives is facial beauty and indeed, as a species, we are very interested in the owners of beautiful faces.

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Our magazines, television, and computer screens are filled with attractive faces and this is not an accident. Such interest in facial beauty raises the main question addressed in this article: why do we find some faces more attractive than others? Despite the speed at which we assess facial beauty, possibly as fast as 1/10th of a second,⁴ the actual traits that make a face attractive are difficult to articulate. One major goal of research on facial attractiveness is to define which facial traits are associated with beauty.

While much research has focused on traits associated with attractiveness, there is another important aspect of research on this topic: why are some traits preferred over others. This is in fact a more complicated question and there are several levels of explanation to address the question, from ultimate explanations, which are theories of why we have such preferences often invoking evolutionary pressures, to proximate explanations, which address the day-to-mechanisms influencing our attraction to particular faces. For example, it has been suggested that

the ultimate function of an attraction to symmetry in faces has resulted from an evolutionary selection pressure to select healthy mates.^{5–7} In this view, individuals who preferred symmetrical faces left behind more offspring than those without such a preference and so preferences for symmetry can increase in a population until everyone has a preference for symmetry. At the proximate level, visual experience is proposed to play a powerful role in what we find attractive, and recent experience of faces can change the types of faces we find attractive.⁸ One further complication to understanding facial attractiveness is that it is clear that not everyone finds the same faces attractive—there is individual variation in the appreciation of facial beauty. Variability and disagreement in judgments of attractiveness can be related to both ultimate and proximate explanations of beauty. In recent years, research on facial attractiveness has embraced the challenge both of determining which face traits are attractive and the various factors that impact on an individual's judgments of attractiveness.

THE IMPACT OF FACIAL BEAUTY

Before we begin to examine the components of facial attractiveness and the mechanisms governing this attraction, it is useful to address whether beauty is important. Given our interest in beautiful faces, it is unsurprising that beauty has a wide variety of impacts on people's lives. For example, beauty is associated with upward economic mobility, especially for women.⁹ Experimental studies have also demonstrated the many advantages of attractiveness. It has long been noted that there exists a 'What is beautiful is good' stereotype,¹⁰ whereby attractive individuals are perceived to possess a variety of positive personality attributions. For example, attractive individuals are thought to be able to achieve more prestigious occupations, be more competent spouses with happier marriages and have better prospects for personal fulfillment.¹⁰ There have been a large number of studies examining this attractiveness stereotype, demonstrating that attractive people are seen in positive light for a wide range of attributes compared with unattractive people. In mock interviews, attractive people are more likely to be hired than less attractive individuals¹¹ and attractiveness can also influence judgments about the seriousness of committed crimes.¹² Outside the laboratory, attractive people also appear to lead favorable lives; attractive individuals pay lower bail¹³ and are more likely to be hired for jobs¹⁴ than less attractive individuals. So, not only are there consistent associations between positive traits and attractiveness (see Refs 15 and 16 for

meta-analytic reviews of research on physical attractiveness stereotypes), attractive people also appear to have many social advantages in their everyday lives. The impact of facial attractiveness is not restricted to adulthood; mothers are more nurturing to attractive babies than unattractive babies.¹⁷ Overall, it is clear that attractive people appear to be treated differently to unattractive people despite a prevalent belief, at least in Western society, that one 'should not judge a book by its cover'.

IS THERE SUCH A THING AS ATTRACTIVENESS?

Exactly what makes a particular face attractive is poorly defined. In fact, the well-known phrase 'beauty is in the eye of the beholder' is a testament to our belief that attractiveness is ephemeral. For example, the philosopher David Hume is often quoted for making the argument that beauty, 'is no quality in things themselves: it exists merely in the mind which contemplates them; and each mind contemplates a different beauty'¹⁸ (p. 208–209). Darwin¹⁹ was also struck by cultural differences, such as preferences for skin color, body hair, body fat, and practices such as lip ornamentation and teeth filing, 'It is certainly not true that there is in the mind of man any universal standard of beauty with respect to the human body'. While individual and cross-cultural differences exist (discussed later), it appears, however, that there are certain features of faces that are attractive across observers. In fact, agreement between individuals is well-documented. Across many studies, it has been found that there is a high degree of agreement from individuals within a particular culture and also high agreement between individuals from different cultures (see Ref 16 for a meta-analytic review). If different people can agree on which faces are attractive and which faces are not attractive when judging faces of varying ethnic background, then this suggests that people everywhere are all using the same, or at least similar, criteria in their judgments. Further evidence for universal attractiveness criteria comes from studies of infants. When infants (3–6 months of age) are shown faces that have been judged by adults for attractiveness, they prefer to look at faces that are rated more highly for attractiveness than at those faces rated lower.^{20,21} It therefore appears that before any substantial exposure to cultural standards of attractiveness, infants demonstrated a preference for attractive faces that are in agreement with adult judgments. It has been suggested that there is something innate about attractiveness, and that human children (and adults) have a biologically based, universal attractiveness detector.²²



FIGURE 1 | Female students versus model/celebrity composites. The picture on the left is made up of images of models and celebrities. The picture on the right is made up of images of students. People will generally agree on which of this pair is the most attractive.

These studies suggest that attractiveness is recognized at a much earlier age than most would expect and that, contrary to popular belief, there is much agreement in what is and what is not attractive about faces across human cultures. Both early developmental and cross-cultural agreement on attractiveness are evidence against the notion that attractiveness ideals are slowly absorbed by those growing up within a particular culture, and this suggests that there is something universal about attractive faces (and unattractive faces) that are recognized both across individuals and cultures, in adults and in infancy (Figure 1).

WHY DO WE CARE ABOUT ATTRACTIVENESS?

The impact of attractiveness on our behavior toward others may appear puzzling if attractiveness is without meaning. If attractiveness serves an important function, then this behavior becomes less puzzling. Evolutionary theory has been proposed to be able to cast light on what features are attractive and what makes people seek out and desire to mate with attractive individuals. The two major problems faced by an organism are survival and reproduction, and it is *differential reproductive success* that is the key to evolution. The evolutionary view suggests that choosiness may reflect preferences that drive us to acquire high-quality mates—the traits we find attractive in individuals may be directly linked to their value as mates.²³ High-quality/value mates are those who can best enhance the reproductive success of a potential partner. Women and men should both be sensitive to cues that indicate higher mate value because individuals who were attentive to cues of high mate value, and based mate-choice decisions on them, left behind

more offspring, which would be healthier and more fecund, than those who failed to attend to these cues. Darwin¹⁹ was the first to point to a force he called sexual selection to account for the seemingly inexplicable differences between the sexes of some species and suggested that sexual selection arises from differences in reproductive success caused by competition over mates. Examples of sexual selection can be seen in such traits as the antlers of stags, peacock's tails, bird song, and the extravagant colors of many species of birds and fish. These traits have no obvious input into the survival of an organism, and in fact many of them prove detrimental to the survival of the possessor, and at the very least have a cost to the individual to produce them. One prominent view is that such traits may act as indicator mechanisms, indicating the possession of, for example, good genes. There is a distinction among the benefits acquired from mating with individuals in possession of good genes. Two types of advantage are possible: indirect benefits, acquiring good genes from partners that benefit offspring, and direct benefits, acquiring factors other than good genes from partners that benefit the choosing individual. For example, choosing a healthy partner may lead to offspring inheriting genes resistant to disease and avoiding a parasitized mate has obvious direct advantages whether parasite resistance is heritable or not.

Research has highlighted the potential benefits associated with mating and reproducing with an attractive partner. For example, individuals with attractive faces have been found to live longer²⁴ and produce more children^{25,26} than individuals with less attractive faces. Individuals who partner with attractive-faced people are then likely to produce more children and have a long-lived partner who can invest in themselves and their offspring. Furthermore, if all of these traits are heritable, then those who can select attractive-faced partners will also produce offspring who are attractive, long-lived, and who will themselves produce more children. Research has also linked attractiveness to other biological and reproductively relevant factors, such as hormones. For example, cortisol, a hormone that is found at higher concentrations in humans under stressful conditions, has been found to be lower in women with attractive faces.²⁷ In other studies, women's faces have been found to be more attractive at peak fertility in the menstrual cycle,²⁸ a time when reproductive hormones such as estrogen are high, than at other times. A similar result is also seen across women controlling for cycle stage. Women's facial attractiveness is positively related to their levels of estrogen.²⁹ These findings together suggest that selection of attractive-faced women could lead men to select women who are less stressed and

who are more likely to become pregnant. Men who select attractive-faced women may then benefit by producing more offspring more quickly and by having partners more capable of devoting time to investing in them.

Overall, an evolutionary view assumes that perception and preferences serve an adaptive function: the external world provides information to guide biologically and socially functional behaviors.³⁰ If in our evolutionary past, information was present about a person's value (e.g., genetic quality) in any way, then an advantage would accrue for those who utilized these signs and those individuals would leave more genes behind in the next generation. Theoretically then, our facial preferences guide us to choose mates who will provide the best chance of our genes surviving. This gives us an answer to why attractiveness is so important: there are potentially important reproductive consequences based on our preferences. In the section on *Face Traits Associated with Beauty*, I discuss some of the traits that have been studied in terms of their influence on attraction.

FACE TRAITS ASSOCIATED WITH BEAUTY

Faces vary in many different ways and many of these variations impact on the judgment of attractiveness. In this section, I describe some of the facial traits that are proposed to relate to the perception of beauty and present the reasoning for why each is thought to be associated with attractiveness.

Youth

Faces change with age, e.g., becoming more wrinkled as skin loses elasticity. Youth is generally seen as a desired trait in potential partners,³¹ and individuals rate younger appearing faces as more attractive than older faces.³² In evolutionary terms, preferences for youthful partners can provide several important benefits. For example, youth is associated with vigor and a longer period of potential parental investment. Furthermore, at least in women, youth is strongly associated with the ability to produce offspring over time—younger women can produce more offspring than older women because women do not reproduce after menopause.

Weight

Faces also contain cues to body weight. Much research has examined the role of body weight on judgments of attractiveness. In many Western societies, thinness

appears to be a valued trait. Women with low body mass indices (a standard measure of weight, calculated by dividing weight by height),² receive higher attractiveness ratings.³³ Associations between thinness and attractiveness do not appear to be sex-specific. Thinner men also receive higher ratings of social desirability and attractiveness compared with heavier men.³⁴ Perceived weight in faces, or facial adiposity, has been linked to perceived attractiveness, in the same direction as studies of body weight, as well as health measures,³⁵ indicating that attraction to weight in faces may reflect preferences for healthy partners. Following this link, some research has also shown that facial adiposity relates to markers of immune system quality.³⁶

Color

Facial coloration is directly related to the appearance of facial skin. In research on non-human primates, experimental manipulation of color shows that female rhesus macaques prefer images of redder male faces.³⁷ While some studies suggest that the color red may be seen as a threatening stimulus in humans,³⁸ red also appears to enhance attraction in some instances. For example, women are seen as more attractive by men when presented with red backgrounds or with red clothing, relative to other colors.³⁹ Further research has examined red coloration in human faces and demonstrated a positive association with perceived health.⁴⁰ The authors suggest that perception of healthy, oxygenated blood may drive associations between red and healthiness. Alongside redness, people also think that skin yellowness is associated with healthy appearance in faces.⁴⁰ Yellowness may advertise health via an association with good diet, as carotenoids are associated with skin yellowness and are absorbed via the intake of fruits and vegetables.⁴⁰ Taken together, these studies suggest that information on attractiveness and health is available from surface skin coloration.

Averageness

The averageness of a face is related to how closely it resembles the majority of other faces within a population. Average faces are not distinctive and non-average faces have more extreme and recognizable characteristics. Average faces are proposed to be attractive because the possession of features that are close to a population average in shape, size, or configuration is potentially linked to genetic diversity.⁴¹ For example, it has been argued that average faces may be attractive because the owners of average faces possess a diverse set of genes that may lead to better resistance

to common pathogens.⁴¹ Averageness is associated with facial attractiveness. Galton⁴² was one of the first to propose that facial attractiveness may relate to facial averageness. When using photographic superimposing techniques to combine facial images, he noted that the faces created from this blending were more attractive than the constituent faces. Recent studies have improved upon these techniques using computer graphic techniques. Work by Langlois and Roggman^{22,43} has shown that these composite faces are judged to be more attractive than the individual faces that they are made up from. Caricaturing has also been used to study the attractiveness of averageness. A caricature exaggerates the differences between an individual face and an average face thereby reducing the averageness of the original. Using this technique, Rhodes and Tremewan⁴⁴ found that higher averageness was associated with higher attractiveness using this technique (see Figure 2). It has been pointed out that composite faces possess a high degree of bilateral symmetry as well as possessing features that are close to a population average.⁴⁵ Other studies have used perfectly symmetric images manipulated in averageness and still have demonstrated preferences for averageness.^{46,47} It has also been noted that in the original composite studies, the more images that are blended together, the more the skin texture becomes smoother as imperfections such as lines or blemishes are also averaged.⁴⁵ Skin color/texture has been controlled in studies that normalize the texture/color of all the faces seen, and these studies all also demonstrate that average is attractive.^{44,46–48} While the majority of the work described above has been carried out in

North America, Britain, and Australia, averageness has also been found to be attractive across different cultures. For example, averageness is also found attractive in Japanese participants⁴⁹ and in African hunter-gatherers.⁴⁷ Overall, there is clear evidence that averageness is an important determinant of facial attractiveness.

Symmetry

Symmetry refers to the extent that one half of an image (e.g., organism) is the same as the other half. Much work has been done on morphological symmetry and sexual selection in other animals, and this forms the basis of theories of symmetry preferences in humans. Individuals differ in their ability to maintain the stable development of their morphology under the prevailing environmental conditions under which that development is taking place.⁵⁰ The ability of an individual to develop successfully in the face of environmental pressures, associated with lower asymmetry, is therefore one proposed indicator of genetic quality. Indeed, symmetric men and women have been found to be healthier than their more asymmetric peers.⁵¹ Studies of naturally occurring human facial asymmetries provide evidence that symmetry is found attractive, although such studies can be confounded by potential correlates. Grammer and Thornhill⁵² measured asymmetry, using points marked on facial images, and found that the horizontal symmetry of the faces was positively correlated with attractiveness judgments of both male and female faces. Several studies using manipulated faces have also demonstrated that symmetry can

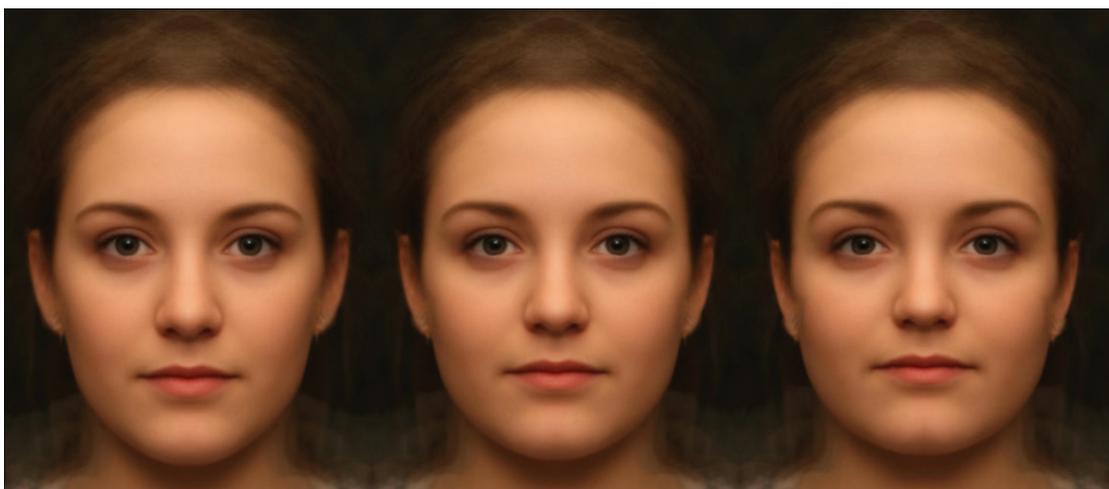


FIGURE 2 | Caricaturing can decrease averageness. If we calculate the average shape of a number of faces, we can define an average face shape. By manipulating a particular face either toward or away from this average, we can increase or decrease averageness. From left to right: original composite image, +40% distinctive, +80% distinctive. These images have been perfectly symmetric and a composite image has been used to protect the identity of the individuals. The images should look less attractive as averageness decreases and distinctiveness increases.



FIGURE 3 | Computer graphic manipulations of shape masculinity and femininity. From left to right: 50% feminine, original composite image, +50% masculine. These images are made using the shape difference between a composite male and a composite female image.⁶⁰ Increasing femininity in female faces generally increase attractiveness. Studies show that some people like feminine men and some people like masculine men, while others have no particular preference.

have a positive influence on attractiveness.^{53,54} Preferences for symmetry using manipulated faces have also been found in samples of African hunter-gatherers,⁵⁵ and macaque monkeys have also been found to gaze longer at symmetrical than asymmetrical face images of conspecifics.⁵⁶ While the effects of symmetry on attractiveness are relatively small, such effects are found consistently across many studies indicating that symmetry is an attractive facial trait.

Masculinity and femininity

Men and women differ in their size and shape. Mature features in adult human faces reflect the masculinization or feminization of secondary sexual characteristics that occur at puberty. These face shape differences in part arise because of the action of hormones such as testosterone. Consequently, some studies show that more masculine male faces are associated with higher testosterone levels,⁵⁷ while more feminine female faces are associated with higher levels of estrogen.²⁹ Larger

jawbones, more prominent cheekbones, and thinner cheeks are all features of male faces that differentiate them from female faces (see Figure 3). From an evolutionary point of view, extremes of secondary sexual characteristics (more female for women, more male for men) are proposed to be attractive because they advertise the quality of an individual. Sexual dimorphism has been linked to actual health with more masculine-faced men and more feminine-faced women being found to be healthier.⁵¹ There is considerable evidence that feminine female faces are considered attractive. Studies measuring facial features from photographs of women^{52,58,59} and studies manipulating facial composites⁶⁰ all indicate that feminine features increase the attractiveness of female faces across different cultures. If feminine female faces provide cues to fertility and health, then male preferences for such features are potentially adaptive. The link between sexual dimorphism and attractiveness in male faces is less clear. Studies using facial measurements have found that women preferred large jaws in males.^{52,61} Despite

findings showing a preference for more masculine and dominant male faces, several studies have shown that feminine characteristics and faces of low dominance are of increased attractiveness.^{48,60–64} Studies manipulating masculinity and femininity in faces also produce mixed results: several studies have documented preferences for femininity,^{48,63,65,66} but similar computer graphic studies have also reported preferences for masculinity.^{67,68} One explanation may lie in the personality traits masculine- and feminine-faced males are assumed to possess. Increasing the masculinity of face shape increased perceptions of dominance, masculinity, and age but decreased perceptions of warmth, emotionality, honesty, cooperativeness, and quality as a parent.⁶⁰ It appears that socially valued traits such as honesty, warmth, cooperation, and skill as a parent are associated with feminized versions of male faces, while traits such as dominance are associated with masculinized face shapes. Feminization of male face shape may increase attractiveness because it ‘softens’ particular features that are perceived to be associated with negative personality traits. Female face preferences may thus represent a trade-off between the desire for good genes, or other benefits, and the desire for a cooperative partner. This trade-off means that masculinity in male faces may be more or less attractive under certain contexts and to certain individuals generating variation.

Health

Perhaps unsurprisingly, people find healthy appearing faces attractive. Perceived health is difficult to relate to any one metric, but people will readily rate faces for perceived health and show very high agreement on such ratings.^{69,70} In evolutionary terms, there is a large and obvious selective advantage in detecting healthy partners for both social exchange and mate choice. Again, as for previous traits, there may be both direct and indirect benefits to partnering with individuals who are perceived to be healthy. One study has examined how well ratings of health from small patches of skin of faces are related to overall rated attractiveness when the whole face image is available. Apparent health of facial skin is positively correlated with ratings of male facial attractiveness.⁷¹ Skin health may be a particularly useful marker of current health condition as it is more changeable than aspects such as symmetry or averageness.

‘Good’ behavior and personality

Personality traits are reported cross-culturally to be among the most important factors in partner choice by both sexes.⁷² If desired personality is important,

it would appear likely that personality attributions elicited by a person’s face would affect their attractiveness. For example, women who value cooperation and good parenting may avoid masculine-faced men who are perceived to be more dominant and less good at parenting than feminine-faced men. Indeed, individuals may use personality stereotypes in mate selection to select partners with a personality that they desire. Some perceptual attributions to facial photographs are somewhat accurate,⁷³ and so choosing a partner based on perceived personality may result in acquiring a partner who actually possesses desired personality traits. One study has indeed demonstrated that a desire for some personality traits influences judgments of facial attractiveness.⁷⁴ Individuals valuing particular personality traits find faces appearing to display these traits attractive. Conversely, those not valuing particular traits find faces attractive that are perceived to possess that trait less. Thus, desired personality influences perceptions of facial attractiveness in opposite-sex faces, suggesting that ‘what is good is beautiful.’⁷⁴ Related to personality, positive expressions like smiling have also been found to have a positive impact on attractiveness.⁷⁵ In terms of benefits to perceivers, it is easy to see why traits such as appearing trustworthy would make a face appear more attractive. For individual-specific traits, the logic is more complicated, but such preferences could be related to behavioral compatibility within couples, as people do tend to desire partners with personalities similar to their own.⁷⁶ It is also clear that people desire certain positive personality traits, such as warmth, in faces.⁷⁶

PROXIMATE MECHANISMS AFFECTING ATTRACTION

While many traits are linked to facial attractiveness, as reviewed above, preferences are underpinned by a wide variety of cognitive mechanisms which themselves may be affected by experience or other internal factors. In this section, I discuss some examples of factors that can increase or decrease liking and attraction that relate to variables that do not necessarily involve particular traits but instead are based on other factors. These factors could also be viewed as proximate causes of attraction, part of the mechanisms via which we find others more or less attractive.

Familiarity

Familiarity is a powerful determinant of attraction and the more we see something, generally, the more we like it (i.e., the mere exposure effect⁷⁷). For many types of stimuli, exposure increases attraction even

when the exposure is unconscious.^{78,79} Familiarity, when not paired with aversive stimuli, is thought to be rewarding,⁷⁹ and there are obvious benefits to avoiding unfamiliar people because such individuals are unpredictable and could prove dangerous. Indeed, approaching the unfamiliar with caution is likely an adaptive response as this response prepares individuals for danger. Through familiarity, the unpredictable comes to be seen as predictable and safe.⁷⁹ The effects of exposure are demonstrated in recent studies of exposure to faces. After exposure to faces, faces with traits similar to those of previously seen faces come to be more preferred.^{8,80,81} For example, if a person is exposed to faces with wide-set eyes, then new faces that possess wide-set eyes are found more attractive than if a person is exposed to narrow-set eyes.

Reinforcement

Classical conditioning refers to stimuli–reward associations. For example, if the sound of a bell is contingently paired with a food reward, the sound of the bell can come to be associated with the positive reward of food. Such effects are extremely powerful and researchers have proposed that our attraction to others may also reflect such conditioning. In a *reinforcement-affect* model,⁸² it has been argued that individuals can become associated with reward or punishment too. In a simple example of unpleasant conditions leading to a lack of liking, individuals rated fictitious strangers as less attractive if the person judging is made to feel too hot by increasing room temperature or feel crowded by squashing more people into a space.⁸³ More recent studies have demonstrated that positive or negative association can affect face preferences, with positive experiences (faces paired with pleasant sounds) leading to increased attraction and negative experiences (faces paired with unpleasant sounds) leading to decreased attraction.⁸⁴ Interestingly, the effects of positive reward do not just apply to the specific individuals who were paired with the positive/negative stimuli, the effects of reward pairing generalize to judgments of novel, physically similar individuals.⁸⁴

Physiological Arousal

Attraction may also be increased via a misattribution of emotional state. In a classic study, men were approached by a female experimenter to take part in a study either on a high suspension bridge (fear-arousing) or a lower, safer appearing bridge (non-fear-arousing), in which the experimenter gave the man a phone number by which they could attempt to contact her later for more information. Those men

approached in the high arousal situation were found to be more likely to attempt to contact the interviewer than those in the low arousal condition.⁸⁵ This effect was interpreted as the men misattributing the arousal they felt due to being on the high bridge as arousal caused by the interaction with the female experimenter.⁸⁵ Such an interpretation is in line with earlier research demonstrating that when individuals were artificially aroused by administering adrenaline, the lack of an explanation for why they feel aroused can lead to a misattribution to a feeling that they saw another person expressing.⁸⁶ Similar effects have been shown in more recent studies. For example, using running as means to induce arousal, men rating a woman for attractiveness were found to rate already attractive women as more attractive in the high arousal condition.⁸⁷ This effect was reversed when the women being rated was less attractive with lower ratings from men in the high arousal condition, suggesting that misattribution of arousal may polarize opinions. In other words, when attracted to someone, physiological arousal may enhance that attraction, but if not attracted to someone, then arousal may increase a dislike. In a study addressing interactions, strangers were asked to participate in a variety of games with opposite-sex partners, dividing the games into high and low competitive and high and low arousal.⁸⁸ It was found that pairs who participated in high competition/high arousal games showed an increased attraction compared with pairs who participated in low competition/low arousal games.⁸⁸

BEAUTY IN THE EYE OF THE BEHOLDER

In the section on *Proximate Mechanisms Affecting Attraction*, I reviewed some factors that impact on attraction at the proximate level. Despite broad agreement on attractiveness, there are many other factors that may influence an individual in determining who they find attractive. In this section, I review some examples of areas in which variation has been examined.

Sex Differences

Women and men may differ in the relative importance they place on certain traits.⁸⁹ Of course, both men and women value physical attractiveness, and other positive traits, in a partner. However, the relative balance of certain preferences may not be equal, with members of one sex placing more importance on some traits compared with the other. For example, women value earning potential and ambition/drive

more than men do.⁷² Conversely, men value youth and attractiveness more than women do.⁷² Indeed, research on sex differences in age preferences demonstrated that women desire a slightly older man, while men desire younger women.³¹ In general, these sex differences are in line with a difference in priorities related to what is important to each sex. Women value wealth/status more than men as these traits have more bearing on their ability to produce offspring than the attractiveness of the man. Men, on the other hand, value youth and beauty more than women because there is a stronger relationship between age and the ability to produce children in women than in men.

Within-Person Differences

What a person finds attractive may change over time or depending on context. In this way, the same person may find different faces attractive depending on a variety of factors. For example, several studies have demonstrated that women's preferences for various traits change across the menstrual cycle. One of the most well-documented phenomena in studies examining cyclical preference shifts is a greater attraction to masculine male faces (see Figure 3) at peak fertility in the menstrual cycle,^{90–94} a within-individual shift driven by variation in hormone levels across the cycle. This shift has been proposed to be adaptive in changing the preferences of women when they are most likely to become pregnant toward high-quality men, or in leading to attraction to more cooperative men when they are not likely to become pregnant.^{90–94} As a different, but potentially complementary, explanation for shifting preferences, rather than acquiring direct benefits for offspring from masculine men, women may maximize investment from feminine men when raised progesterone prepares the body for pregnancy.⁹⁵

A related difference in preference is seen when asking people to judge faces for attractiveness in different relationship contexts. For short-term relationships, women are more likely to choose an attractive man who is less cooperative with worse parenting qualities over a less attractive man who is more cooperative and with better parenting qualities.⁹⁶ In contrast, in long-term contexts women choose the less attractive but more cooperative man more often.⁹⁶ In face preferences, women judging men for short-term relationships prefer more masculinity in faces than those judging for long-term relationships.⁶⁶ These findings are consistent with the hypothesis that masculinity in men is associated with indirect genetic benefits to offspring: when investment is not an issue, as in short-term relationships, traits associated with

indirect benefits would be expected to be valued more highly. In the context of a long-term relationship, however, where investment is an issue, women may change their priorities and prefer cues to long-term investment, which are not necessarily consistent with traits that indicate high genetic quality.

Between-Person Differences

Preference may also vary according to the traits of the particular observer. For example, several studies have suggested that preferences may be influenced by one's own attractiveness. Condition-dependent mate choice is seen in female fish of several species, whereby higher quality females are more attentive to cues to male quality.⁹⁷ In humans, condition-dependent mate choice is potentially adaptive for women of low mate value in order to avoid the costs of decreased parental investment/potential desertion from high-quality partners.⁶⁵ Such reasoning arises from notions that high-quality males are least likely to invest in or most likely to desert their partners.⁹⁸ Little et al.⁶⁵ found that women who thought they were physically attractive preferred more masculine faces and had greater preferences for symmetry than those women who thought they were less physically attractive. Subsequent studies have shown similar effects using more objective measures of attractiveness, such as other-rated facial attractiveness and measures of body shape related to attractiveness.^{99,100} There are of course other individual factors that can influence preferences, such as the desire for certain personality traits discussed earlier.

Cultural Differences

There are many potential differences between cultures, and one aspect that has received attention in terms of explaining variation in preferences between cultures is pathogen or disease risk. In an environment with a high risk of pathogens, the probability of offspring survival and eventual reproduction decreases. Consequently, there may be few benefits to attracting an attentive/investing partner because individuals may maximize their reproductive output by focusing on acquiring good genes for their offspring.¹⁰¹ Penton-Voak et al.¹⁰² found stronger preferences for male masculinity in Jamaicans than in the UK and Japan, and suggested that a higher pathogen prevalence may result in increased preferences for masculinity in male faces. The Hadza, a tribe of African hunter-gathers, have also been found to exhibit stronger preferences for facial symmetry than do participants in the UK.⁵⁵ Another study examined a

larger cross-cultural sample of 30 countries, calculating both the average female preference for male facial masculinity (Figure 3) and a composite health index derived from World Health Organization statistics.¹⁰³ This study found that poorer health (i.e., higher mortality and incidence of disease) was related to stronger female preferences for male masculinity.¹⁰³ All of these studies are suggestive that under conditions of health risk, preferences for healthy, masculine partners are stronger, reflecting motivations to secure direct or indirect benefits.

Another source of variation between cultures may arise from social learning. Individuals often learn from others, and selection for social learning mechanisms may occur when there are costs to acquiring accurate information via individual learning.¹⁰⁴ Inspired by work on non-human species, recent research also suggests that social learning may influence human mate preferences.¹⁰⁵ Modeling work has shown that social transmission of preferences in humans can result in a directional pressure on both traits and preferences within populations, and this could account for genetically based phenotypic variation between cultures.¹⁰⁶ For example, if a preference for large noses arose within a population, other members and subsequent members of that population would observe the preferences and learn that the trait was attractive, perpetuating a preference for large noses through a population and maintaining the preference over generations. These effects may help explain the diversity of preferences for seemingly arbitrary traits seen across cultures, such as facial tattooing or scarification.

CONCLUSION

Facial attractiveness has important social consequences. While there is a widespread belief that beauty cannot be defined, in fact, there is considerable agreement across individuals and cultures (and sometimes species) on what is found attractive. The power of facial beauty is compelling and human interest in attractiveness appears similar to the interest that non-human animals display in their mate preferences.

By considering that attraction and mate choice are critical components of evolutionary selection, we can perhaps better understand the importance of beauty. There are clearly many traits that are linked to facial attractiveness in humans and each may in some way impart direct or indirect benefits to individuals who act on their preferences. If a trait is reliably associated with some benefit to the perceiver, then we would expect individuals in a population to find that trait attractive. Such an approach has highlighted traits such as age, health, symmetry, and averageness of faces. This evolutionary view may postulate that some traits will be universally attractive; however, this does not preclude interesting variation. Indeed, it would be surprising in a true evolutionary perspective that there existed a template of a perfect mate that was not affected by experience, environment, context, or the specific needs of an individual. Research on facial attractiveness has documented how various face traits are associated with attractiveness and various factors that impact on an individual's judgments of attractiveness.

In recent years, there have been many advances in the study of facial attractiveness, for example, in the use of sophisticated computer graphic techniques to manipulate specific aspects of facial appearance. In the future, studies are likely to include the use of more ecologically valid stimuli such as 3D faces¹⁰⁷ and moving faces¹⁰⁸. Furthermore, there is a rich seam of possibilities in understanding how facial information is integrated with other factors that are associated with attractiveness, such as voices.¹⁰⁹ Overall, facial attractiveness is complex, both in the number of traits that determine attraction and in the large number of factors that can alter attraction to particular faces, such as recent experience or even how attractive the observer is. A fuller understanding of facial beauty will come with an understanding of how these various factors interact with each other. This understanding will be further enriched by embracing new technologies to study face perception and by examining how facial information interacts with other types of social information.

REFERENCES

1. Little AC, Jones BC, DeBruine LM. The many faces of research on face perception introduction. *Philos Trans R Soc B* 2011, 366:1634–1637.
2. Johnson MH, Dziurawiec S, Ellis H, Morton J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 1991, 40:1–19.
3. Goren CC, Sarty M, Wu PYK. Visual following and pattern discrimination of face like stimuli by newborn infants. *Paediatrics* 1975, 56:544–549.
4. Willis J, Todorov A. First impressions: making up your mind after a 100-ms exposure to a face. *Psychol Sci* 2006, 17:592–598.

5. Thornhill R, Gangestad SW. Facial attractiveness. *Trends Cogn Sci* 1999, 3:452–460.
6. Rhodes G. The evolutionary psychology of facial beauty. *Annu Rev Psychol* 2006, 57:199–226.
7. Little AC, Jones BC, DeBruine LM. Facial attractiveness: evolutionary based research. *Philos Trans R Soc B* 2011, 366:1638–1659.
8. Rhodes G, Jeffery L, Watson TL, Clifford CWG, Nakayama K. Fitting the mind to the world: face adaptation and attractiveness aftereffects. *Psychol Sci* 2003, 14:558–566.
9. Elder GHJ. Appearance and education in marriage mobility. *Am Sociol Rev* 1969, 34:519–533.
10. Dion K, Berscheid E, Walster E. What is beautiful is good. *J Pers Soc Psychol* 1972, 24:285–290.
11. Cash TF, Kilcullen RN. The eye of the beholder—susceptibility to sexism and beautyism in the evaluation of managerial applicants. *J Appl Soc Psychol* 1985, 15:591–605.
12. Sigall H, Ostrove N. Beautiful but dangerous: effects of offender attractiveness and nature of the crime on juridical judgement. *J Pers Soc Psychol* 1975, 31:410–414.
13. Downs AC, Lyons PM. Natural observations of the links between attractiveness and initial legal judgments. *Pers Soc Psychol Bull* 1991, 17:541–547.
14. Chiu RK, Babcock RD. The relative importance of facial attractiveness and gender in Hong Kong selection decisions. *Int J Hum Resour Manage* 2002, 13:141–155.
15. Eagly AH, Ashmore RD, Makhijani MG, Longo LC. What is beautiful is good, but ...: a meta-analytic review of research on the physical attractiveness stereotype. *Psychol Bull* 1991, 110:109–128.
16. Langlois JH, Kalakanis L, Rubenstein AJ, Larson A, Hallamm M, Smoot M. Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychol Bull* 2000, 126:390–423.
17. Langlois JH, Ritter J, Casey J, Solwin D. Infant attractiveness predicts maternal behaviours and attitudes. *Dev Psychol* 1995, 31:464–472.
18. Hume D. *Four Dissertations. IV: Of the Standard of Taste*. London: Millar; 1757.
19. Darwin C. *The Descent of Man, and Selection in Relation to Sex*. 1st ed. London: John Murray; 1871.
20. Langlois JH, Roggman LA, Casey RJ, Ritter JM, Riser-Danner LA, Jenkins VY. Infant preferences for attractive faces: rudiments of a stereotype? *Dev Psychol* 1987, 23:363–369.
21. Samuels CA, Butterworth G, Roberts T, Graupner L, Hoyle G. Facial aesthetics: babies prefer attractiveness to symmetry. *Perception* 1994, 23:823–831.
22. Langlois JH, Roggman LA. Attractive faces are only average. *Psychol Sci* 1990, 1:115–121.
23. Symons D. An evolutionary approach: can Darwin's view of life shed light on human sexuality? In: Geer JH, O'Donohoe WT, eds. *Theories of Human Sexuality*. New York: Plomin Press; 1987, 91–126.
24. Henderson JJA, Anglin JM. Facial attractiveness predicts longevity. *Evol Hum Behav* 2003, 24:351–356.
25. Pflueger LS, Oberzaucher E, Katina S, Holzleitner IJ, Grammer K. Cues to fertility: perceived attractiveness and facial shape predict reproductive success. *Evol Hum Behav* 2012, 33:708–714.
26. Jokela M. Physical attractiveness and reproductive success in humans: evidence from the late 20th century United States. *Evol Hum Behav* 2009, 30:342–350.
27. Rantala MJ, Coetsee V, Moore FR, Skrinda I, Kecko S, Krama T, Kivleniece I, Krams I. Facial attractiveness is related to women's cortisol and body fat, but not with immune responsiveness. *Biol Lett* 2013, 9:20130255.
28. Roberts SC, Havlicek J, Flegr J, Hruskova M, Little AC, Jones BC, Perrett DI, Petrie M. Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proc R Soc Lond B Biol* 2004, 271:S270–S272.
29. Law-Smith MJ, Perrett DI, Jones BC, Cornwell RE, Moore FR, Feinberg DR, Boothroyd LG, Durrani SJ, Stirrat MR, Whiten S, et al. Facial appearance is a cue to oestrogen levels in women. *Proc R Soc Lond B Biol* 2006, 273:135–140.
30. Zebrowitz-McArthur L, Baron RM. Toward and ecological approach to social perception. *Psychol Rev* 1983, 90:215–238.
31. Kenrick DT, Keefe RC. Age preferences in mates reflect sex differences in human reproductive strategies. *Behav Brain Sci* 1992, 15:75–133.
32. Korthase KM, Trenholme I. Perceived age and perceived physical attractiveness. *Percept Mot Skills* 1982, 54:1251–1258.
33. Tovee MJ, Reinhardt S, Emery JL, Cornelissen PL. Optimum body-mass index and maximum sexual attractiveness. *Lancet* 1998, 352:548.
34. Wade TJ, Fuller L, Bresnan J, Schaefer S, Mlynarski L. Weight halo effects: individual differences in personality evaluations and perceived life success of men as a function of weight? *Pers Individ Dif* 2007, 42:317–324.
35. Coetsee V, Perrett DI, Stephen ID. Facial adiposity: a cue to health? *Perception* 2009, 38:1700–1711.
36. Rantala MJ, Coetsee V, Moore FR, Skrinda I, Kecko S, Krama T, Kivleniece I, Krams I. Adiposity, compared with masculinity, serves as a more valid cue to immunocompetence in human mate choice. *Proc R Soc Lond B Biol* 2013, 280:20122495.
37. Waitt C, Little AC, Wolfensohn S, Honess P, Brown AP, Buchanan-Smith HM, Perrett DI. Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proc R Soc Lond B Biol Sci* 2003, 270:S144–S146.

38. Little AC, Hill RA. Social perception of red suggests special role in dominance signalling. *J Evol Psychol* 2007, 1–4:161–168.
39. Elliot AJ, Niesta D. Romantic red: red enhances men's attraction to women. *J Pers Soc Psychol* 2008, 95:1150–1164.
40. Stephen ID, Smith MJL, Stirrat MR, Perrett DI. Facial skin coloration affects perceived health of human faces. *Int J Primatol* 2009, 30:845–857.
41. Thornhill R, Gangestad SW. Human facial beauty: averageness, symmetry, and parasite resistance. *Hum Nat* 1993, 4:237–269.
42. Galton FJ. Composite portraits. *Nature* 1878, 18:97–100.
43. Langlois JH, Roggman LA, Musselman L. What is average and what is not average about attractive faces. *Psychol Sci* 1994, 5:214–220.
44. Rhodes G, Tremewan T. Averageness, exaggeration, and facial attractiveness. *Psychol Sci* 1996, 7:105–110.
45. Alley TR, Cunningham MR. Averaged faces are attractive, but very attractive faces are not average. *Psychol Sci* 1991, 2:123–125.
46. Jones BC, DeBruine LM, Little AC. The role of symmetry in attraction to average faces. *Percept Psychophys* 2007, 69:1273–1277.
47. Apicella CL, Little AC, Marlowe FW. Facial averageness and attractiveness in an isolated population of hunter-gatherers. *Perception* 2007, 36:1813–1820.
48. Little AC, Hancock PJB. The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *Br J Psychol* 2002, 93:451–464.
49. Rhodes G, Yoshikawa S, Clark A, Lee K, McKay R, Akamatsu S. Attractiveness of facial averageness and symmetry in non-Western populations: in search of biologically based standards of beauty. *Perception* 2001, 30:611–625.
50. Møller AP, Swaddle JP. *Asymmetry, Developmental Stability, and Evolution*. Oxford: Oxford University Press; 1997.
51. Thornhill R, Gangestad SW. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evol Hum Behav* 2006, 27:131–144.
52. Grammer K, Thornhill R. Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *J Comp Psychol* 1994, 108:233–242.
53. Perrett DI, Burt DM, Penton-Voak IS, Lee KJ, Rowland DA, Edwards R. Symmetry and human facial attractiveness. *Evol Hum Behav* 1999, 20:295–307.
54. Rhodes G, Proffitt F, Grady J, Sumich A. Facial symmetry and the perception of beauty. *Psychon Bull Rev* 1998, 5:659–669.
55. Little AC, Apicella CL, Marlowe FW. 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 Lond B Biol* 2007, 274:3113–3117.
56. Waitt C, Little AC. Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. *Int J Primatol* 2006, 27:133–145.
57. Penton-Voak IS, Chen JY. High salivary testosterone is linked to masculine male facial appearance in humans. *Evol Hum Behav* 2004, 25:229–241.
58. Cunningham MR. Measuring the physical in physical attractiveness: quasi-experiments on the sociobiology of female facial beauty. *J Pers Soc Psychol* 1986, 50:925–935.
59. Jones D, Hill K. Criteria of facial attractiveness in five populations. *Hum Nat* 1993, 4:271–296.
60. Perrett DI, Lee KJ, Penton-Voak IS, Rowland DR, Yoshikawa S, Burt DM, Henzi SP, Castles DL, Akamatsu S. Effects of sexual dimorphism on facial attractiveness. *Nature* 1998, 394:884–887.
61. Cunningham MR, Barbee AP, Pike CL. What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *J Pers Soc Psychol* 1990, 59:61–72.
62. Berry DS, McArthur LZ. Some components and consequences of a babyface. *J Pers Soc Psychol* 1985, 48:312–323.
63. Rhodes G, Hickford C, Jeffery L. Sex-typicality and attractiveness: are supermale and superfemale faces super-attractive. *Br J Psychol* 2000, 91:125–140.
64. Swaddle JP, Reiersen GW. Testosterone increases perceived dominance but not attractiveness in human males. *Proc R Soc Lond B Biol* 2003, 269:2285–2289.
65. Little AC, Burt DM, Penton-Voak IS, Perrett DI. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc R Soc Lond B Biol* 2001, 268:39–44.
66. Little AC, Jones BC, Penton-Voak IS, Burt DM, Perrett DI. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc R Soc Lond B Biol* 2002, 269:1095–1100.
67. DeBruine LM, Jones BC, Little AC, Boothroyd LG, Perrett DI, Penton-Voak IS, Cooper PA, Penke L, Feinberg DR, Tiddeman BP. Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proc R Soc Lond B Biol* 2006, 273:1355–1360.
68. Little AC, Mannion H. Viewing attractive or unattractive same-sex individuals changes self-rated attractiveness and face preferences in women. *Anim Behav* 2006, 72:981–987.
69. Jones BC, Little AC, Penton-Voak IS, Tiddeman BP, Burt DM, Perrett DI. Facial symmetry and judgments of apparent health—Support for a 'good genes' explanation of the attractiveness-symmetry relationship. *Evol Hum Behav* 2001, 22:417–429.

70. Jones BC, Perrett DI, Little AC, Boothroyd L, Cornwell RE, Feinberg DR, Tiddeman BP, Whiten S, Pitman RM, Hillier SG, et al. Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proc R Soc Lond B Biol* 2005, 272:347–354.
71. Jones BC, Little AC, Burt DM, Perrett DI. When facial attractiveness is only skin deep. *Perception* 2004, 33:569–576.
72. Buss DM. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behav Brain Sci* 1989, 12:1–49.
73. Borkenau P, Liebler A. Trait inferences: sources of validity at zero acquaintance. *J Pers Soc Psychol* 1992, 62:645–657.
74. Little AC, Burt DM, Perrett DI. What is good is beautiful: face preference reflects desired personality. *Pers Individ Dif* 2006, 41:1107–1118.
75. LaFrance M, Hecht MA. Why smiles generate leniency. *Pers Soc Psychol Bull* 1995, 21:207–214.
76. Botwin MD, Buss DM, Shackelford TK. Personality and mate preferences: five factors in mate selection and marital satisfaction. *J Pers* 1997, 65:107–136.
77. Zajonc RB. Attitudinal effects of mere exposure. *J Pers Soc Psychol* 1968, 9:1–27.
78. Bornstein RF. Exposure and effect: overview and meta-analysis of research 1968–1987. *Psychol Bull* 1989, 106:265–289.
79. Zajonc RB. Mere exposure: a gateway to the subliminal. *Curr Dir Psychol Sci* 2001, 10:224–228.
80. Little AC, DeBruine LM, Jones BC. Sex-contingent face after-effects suggest distinct neural populations code male and female faces. *Proc R Soc Lond B Biol* 2005, 272:2283–2287.
81. Jones BC, DeBruine LM, Little AC. Adaptation reinforces preferences for correlates of attractive facial cues. *Vis Cogn* 2008, 16:849–858.
82. Byrne D, Nelson D. Attraction as a linear function of proportion of positive reinforcements. *J Pers Soc Psychol* 1965, 1:659–663.
83. Griffitt W, Veitch R. Hot and crowded—influences of population density and temperature on interpersonal affective behavior. *J Pers Soc Psychol* 1971, 17:92–98.
84. Jones BC, DeBruine LM, Little AC, Feinberg DR. The valence of experience with faces influences generalized preferences. *J Evol Psychol* 2007, 5:119–129.
85. Dutton DG, Aron AP. Some evidence for heightened sexual attraction under conditions of high anxiety. *J Pers Soc Psychol* 1974, 30:510–517.
86. Schachter S, Singer J. Cognitive, social, and physiological determinants of emotional state. *Psychol Rev* 1962, 69:379–399.
87. White GL, Fishbein S, Rutstein J. Passionate love and the misattribution of arousal. *J Pers Soc Psychol* 1981, 41:56–62.
88. Lewandowski GW, Aron AP. Distinguishing arousal from novelty and challenge in initial romantic attraction between strangers. *Soc Behav Pers* 2004, 32:361–372.
89. Geary DC, Vigil J, Byrd-Craven J. Evolution of human mate choice. *J Sex Res* 2004, 41:27–42.
90. Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa R. Menstrual cycle alters face preference. *Nature* 1999, 399:741–742.
91. Little AC, Jones BC, Burt DM, Perrett DI. Preferences for symmetry in faces change across the menstrual cycle. *Biol Psychol* 2007, 76:209–216.
92. Jones BC, DeBruine LM, Perrett DI, Little AC, Feinberg DR, Smith MJL. Effects of menstrual cycle phase on face preferences. *Arch Sex Behav* 2008, 37:78–84.
93. Little AC, Jones BC. Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context. *Psychoneuroendocrinology* 2012, 37:999–1008.
94. Johnston VS, Hagel R, Franklin M, Fink B, Grammer K. Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evol Hum Behav* 2001, 22:251–267.
95. Jones BC, Little AC, Boothroyd L, DeBruine LM, Feinberg DR, Smith MJ, Cornwell RE, Moore FR, Perrett DI. Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm Behav* 2005, 48:283–290.
96. Scheib JE. Context-specific mate choice criteria: women's trade-offs in the contexts of long-term and extra-pair mateships. *Pers Relat* 2001, 8:371–389.
97. Bakker TCM, Künzler R, Mazzi D. Condition-related mate-choice in sticklebacks. *Nature* 1999, 401:234.
98. Gangestad SW, Simpson JA. The evolution of human mating: trade-offs and strategic pluralism. *Behav Brain Sci* 2000, 23:573–644.
99. Penton-Voak IS, Little AC, Jones BC, Burt DM, Tiddeman BP, Perrett DI. Measures of female condition influence preferences for sexual dimorphism in faces of male *Homo sapiens*. *J Comp Psychol* 2003, 117:264–271.
100. Smith FG, Jones BC, Welling LLW, Little AC, Vukovic J, Main JC, DeBruine LM. Waist-hip ratio predicts women's preferences for masculine male faces, but not perceptions of men's trustworthiness. *Pers Individ Dif* 2009, 47:476–480.
101. Belsky J, Steinberg L, Draper P. Childhood experience, interpersonal development, and reproductive strategy—an evolutionary-theory of socialization. *Child Dev* 1991, 62:647–670.
102. Penton-Voak IS, Jacobson A, Trivers R. Populational differences in attractiveness judgements of male and

- female faces: comparing British and Jamaican samples. *Evol Hum Behav* 2004, 25:355–370.
103. DeBruine LM, Jones BC, Crawford JR, Welling LLM, Little AC. The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proc R Soc Lond B Biol* 2010, 277:2405–2410.
104. Richerson PJ, Boyd R. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago, IL: University of Chicago Press; 2005.
105. Little AC, Jones BC, DeBruine LM, Caldwell CA. Social learning and human mate preferences: a potential mechanism for generating and maintaining between-population diversity in attraction. *Philos Trans R Soc B* 2011, 366:366–375.
106. Laland KN. Sexual selection with a culturally transmitted mating preference. *Theor Popul Biol* 1994, 45:1–15.
107. O'Toole AJ, Price T, Vetter T, Bartlett JC, Blanz V. 3D shape and 2D surface textures of human faces: the role of 'averages' in attractiveness and age. *Image Vis Comput* 1999, 18:9–19.
108. Roberts SC, Saxton TK, Murray AK, Burriss RP, Rowland HM, Little AC. Static and dynamic facial images cue similar attractiveness judgements. *Ethology* 2009, 115:588–595.
109. Feinberg DR, DeBruine LM, Jones BC, Little AC. Correlated preferences for men's facial and vocal masculinity. *Evol Hum Behav* 2008, 29:233–241.

FURTHER READING

Adams R Jr, Ambady N, Nakayama K, Shimojo S, eds. *The Science of Social Vision*. New York: Oxford University Press; 2011.

Little AC, Jones BC, DeBruine LM. Facial attractiveness: evolutionary based research. *Philos Trans R Soc B* 2011, 366:1638–1659.

www.alittlelab.com. (Accessed January 9, 2014).