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Review

Facial attractiveness: evolutionary based research

Anthony C. Little[1,*], Benedict C. Jones[2] and Lisa M. DeBruine[2]

[1]*Department of Psychology, University of Stirling, Stirling FK9 4LA, UK*
[2]*School of Psychology, University of Aberdeen, Aberdeen, UK*

Face preferences affect a diverse range of critical social outcomes, from mate choices and decisions about platonic relationships to hiring decisions and decisions about social exchange. Firstly, we review the facial characteristics that influence attractiveness judgements of faces (e.g. symmetry, sexually dimorphic shape cues, averageness, skin colour/texture and cues to personality) and then review several important sources of individual differences in face preferences (e.g. hormone levels and fertility, own attractiveness and personality, visual experience, familiarity and imprinting, social learning). The research relating to these issues highlights flexible, sophisticated systems that support and promote adaptive responses to faces that appear to function to maximize the benefits of both our mate choices and more general decisions about other types of social partners.

Keywords: attractiveness; mate choice; preferences; agreement; variation; individual differences

1. INTRODUCTION

The human face has been a source of great interest to psychologists and other scientists in recent years because of the extraordinarily well-developed ability of humans to process, recognize and extract information from other's faces (see other papers in this volume). Our magazines and television screens are not just filled with any faces—they are filled with attractive faces, and both women and men are highly concerned with good looks in a potential partner [1]. Physical appearance is important to humans and certain features appear to be found attractive across individuals and cultures [2]. The same holds true across the animal kingdom; most non-human species rely on external traits, such as the size, shape and colour of adornments (e.g. feathers, fur and fins) to attract mates [3]. Research on animals has focused on individual traits that are attractive across individuals, and even species, such as symmetry [4].

Physical attractiveness has important social consequences. For example, beauty is associated with upward economic mobility, especially for women [5,6], attractive people have more dates than less attractive people [7], and people who have dated more attractive individuals report being more satisfied with their dates [8,9]. It has long been noted that there exists a 'What is beautiful is good' stereotype [10] ([2,11,12] for meta-analytical reviews of research on physical attractiveness stereotypes), whereby attractive individuals are perceived to possess a variety of positive personality attributions. In mock interviews, attractive people are more likely to be hired than less attractive individuals [13] and attractiveness can also influence judgements about the seriousness of committed crimes [14]. Outside the laboratory, attractive people also appear to lead favourable lives; attractive individuals pay lower bail [15] and are more likely to be hired for jobs [16,17] than less attractive individuals.

Despite research on social consequences, exactly what it is that makes a face beautiful remains poorly defined. One of the major deterrents in determining the features of an attractive face lies in the widespread belief that standards of attractiveness are learned gradually through exposure to culturally presented ideals (e.g. through the media in Western society) and this has also led to a general belief that cultures vary dramatically in what they perceive to be attractive [18]. If this were true, it would mean that attractiveness is arbitrary and what is beautiful now could, in a different time or place, be considered unattractive. 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' [19, pp. 208–209].

Darwin [20] was also struck by cultural differences, such as those evident in preferences for skin colour, body hair and body fat, and those revealed in practices such as lip ornamentation and teeth filing, 'It is certainly not true that there is in the mind of man any universal standards of beauty with respect to the human body' (Darwin cited by [21]). Such convictions were supported by early cross-cultural work by Ford & Beach [22] who catalogued differences between cultures in preferences for body weight,

* Author for correspondence (anthony.little@stir.ac.uk).

One contribution of 10 to a Theme Issue 'Face perception: social, neuropsychological and comparative perspectives'.

breast size and other aspects of female physique and suggested little consensus.

While individual and cross-cultural differences exist (see later), this politically correct view of beauty is to some extent false. In fact, agreement between individuals is one of the best-documented and most robust findings in facial attractiveness research since the 1970s. 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 [2] for a meta-analytical review). If different people can agree on which faces are attractive and which are not attractive when judging faces of varying ethnic background (e.g. [23]), then this suggests that people everywhere are all using the same, or at least similar, criteria in their judgements.

Cross-cultural agreement on attractiveness is 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 is recognized both across individuals and cultures. In the next section, we discuss traits that are proposed to be generally attractive by reasoning based on evolutionary theories, but we return to the notion of individual variation later. While some traits are proposed to be on average preferred across individuals, an adaptive view of preference suggests that individuals will indeed vary in what they prefer and we examine differences in more detail in §3.

2. THE EVOLUTIONARY BASIS OF ATTRACTION: THE FUNCTIONS OF BEAUTY

An evolutionary view assumes that perception and preferences serve an adaptive function: the external world provides information to guide biologically and socially functional behaviours [24]. If in our evolutionary past, information was present about a person's mate and/or social value (e.g. provisioning ability, genetic quality) in any way, then an advantage would accrue to those who used these signs and those individuals would leave more genes behind in the next generation. Theoretically then, preferences guide us to choose mates who will provide the best chance of our genes surviving. In many studies, this evolutionary view of attractiveness has been used to predict the specific characteristics of attractive faces (see [25] for review). Sexual selection is the theoretical framework for much work and a thorough discussion of this topic in general is beyond the current review. Interested readers can see Andersson [3] for a thorough review, including issues relating to how preferences may arise in populations.

Although we can say whether a face is attractive or unattractive, it is extremely difficult to articulate the specific features that determine this attraction. There are, however, several facial traits that have been proposed to advertise the biological quality of an individual in human faces, and hence to influence attractiveness as a mate: traits such as symmetry, averageness and secondary sexual characteristics (see also [26] for meta-analysis). There are many aspects of 'quality' that can be associated with certain traits but these can be broadly split into two types of benefits to the perceiver: direct benefits, whereby the perceiver directly gains for themselves or their offspring, and indirect benefits, whereby the perceiver gains genetic benefits to their offspring. The former is relevant to both same- and opposite-sex attractiveness judgements, whereas the latter has consequences for reproductive pairings. For example, avoiding a parasitized mate has obvious direct advantages whether parasite resistance is heritable or not [27] as there are direct benefits to choosing a parasite-free mate. Preferences for facial traits that are associated with parasite resistance may be adaptive because this can lead individuals to associate with those who are not carrying contagious parasites (which may be passed on to the individual or to the offspring) and who are able to act as good parents (providing material benefits or care). Individuals who are attracted to those having face traits associated with parasite resistance may also increase the chances of passing on heritable parasite-resistant genes to their offspring. In other words, there are several reasons why avoiding a parasitized mate is advantageous. Ultimately it may be unnecessary to consider the relative weights of indirect and direct benefits; both indirect and direct benefits are likely to be important in evolution and their contributions to attractiveness are difficult to tease apart. We note that much research has focused on women's preferences, although most traits are also relevant for men.

(a) *Symmetry*

Symmetry refers to the extent to which one-half of an object (image, organism, etc.) is the same as the other half. 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 [28,29]. The ability of an individual to develop successfully in the face of environmental pressures is therefore one proposed indicator of genetic quality. A character demonstrates fluctuating asymmetry (FA) when symmetry reflects the normal development, and deviations from this symmetry are randomly distributed with respect to side [30]. FA is a particularly useful measure of developmental stability because we know that the optimal developmental outcome is symmetry. Therefore, any deviation from perfect symmetry can be considered a sub-optimal solution which will result in performance problems in the future. FA is also a useful measure as it subsumes a huge amount of individual variation in development, being the outcome of differences in genetic (e.g. inbreeding, mutation and homozygosity) and environmental (e.g. nutrient intake, parasite load) factors [28,29]. Preferences for symmetry can then, potentially, provide both direct (e.g. by avoiding contagion) and indirect benefits (e.g. by providing healthy genes for offspring) to the perceiver.

Whether symmetry is actually related to quality in other animals and humans is an issue addressed by a large literature, and a complete review is not the focus of this paper. While the issue is divided, and

there is some evidence that symmetry is not associated with quality (e.g. [31]), many studies do show links between symmetry and quality in many species [28,29]. In humans, male body symmetry is positively related to sperm number per ejaculate and sperm speed [32] and female breast symmetry is positively correlated with fecundity [33,34]. Relating to faces, one study has demonstrated that facial asymmetry is positively related to self-reported number of occurrences of respiratory disease [35] and some studies have observed positive correlations between symmetry and other putative indices of underlying physical condition (i.e. exaggerated sex-typical characteristics, [36,37]). The relationship between symmetry and quality is not reviewed in detail here, but it should be noted that fitness-related characteristics, such as growth rate, fecundity and survivability, are positively associated with symmetry across a number of species and taxa (e.g. [29]; see [38] for a review) and ultimately, any link between symmetry and quality, no matter how weak, is sufficient to create a selection pressure on the opposite sex to choose symmetric mates in order to provide genetic quality benefits to their offspring.

In humans, Thornhill & Gangestad [39] found that the total number of sexual partners a man reported having was positively related to skeletal symmetry. Studies of naturally occurring human facial asymmetries also provide evidence that symmetry is found attractive, though such studies can be confounded by potential correlates. Studies measuring symmetry from unmanipulated faces have reported positive correlations with rated attractiveness [40–44] and one study has even demonstrated that with pairs of monozygotic twins, the twin with more symmetric measurements is seen as more attractive [45].

While some studies directly manipulating human facial images have found that asymmetry is preferred to symmetry [46], manipulations used in these studies tend to be crude, using 'chimeric' face images manufactured by aligning one vertically bisected half-face with its mirror reflection. Studies using more sophisticated symmetry manipulations have demonstrated that symmetry can have a positive influence on attractiveness [47,48] and have established that the chimeric manipulations used in the early studies introduced unnatural proportions into the symmetric faces (see [48]). Examples of manipulated images can be seen in figure 1. Thus, the methodologically superior computer graphic studies [47,48] parallel the findings of investigations into naturally occurring facial asymmetries [40,41,43–45]. The computer graphic studies demonstrate that increasing symmetry alone is sufficient to increase attractiveness. Subsequently, other studies have replicated preferences for symmetry using manipulated stimuli in different Western samples (e.g. [49,50]), but evidence for symmetry preferences using these methods is not limited to western populations or even to humans. Preferences for symmetry using manipulated faces have been found in African hunter–gatherers [51], and macaque monkeys gaze longer at symmetrical than at asymmetrical face images of conspecifics [52].

Importantly, recent studies have implicated perceptions of health in attraction to symmetric faces [44,53] and have suggested that the mechanisms underpinning preferences for symmetric faces are different from those that might drive preferences for symmetry in mate-choice-irrelevant stimuli (e.g. [49,50]). Such findings suggest that preferences for symmetric faces reflect, at least in part, adaptations for mate choice.

Figure 1. Symmetry and asymmetry. (*a*) A shape-symmetric facial composite and (*b*) asymmetric version. Features and outline are marked on the faces in order to create symmetric/asymmetric versions. The asymmetric version has had its asymmetry enhanced by 50%. Symmetric images are usually preferred to asymmetric images.

(b) *Averageness*

Averageness refers to how closely a face resembles the majority of other faces within a population; non-average faces have more extreme characteristics than the average of a population. Average faces may be attractive because an alignment of features that is close to a population average is linked to genetic diversity [54,55]. Thornhill & Gangestad [54] have argued that average faces may be preferred to less-average faces because owners of average faces possess a more diverse set of genes, which may result in less common proteins to which pathogens are poorly adapted. Parasites are generally best adapted to proteins that are common in the host population; hence, parasites are adapted to the genes that code for the production of these proteins. A second evolutionary theory for the attractiveness of averageness in faces is that extreme (non-average) genotypes are more likely to be homozygous for deleterious alleles, that is, to be more likely to possess genes that are detrimental to an individual than those with more average genotypes [54]. Both of these theories propose evolutionary benefits to mating with individuals possessing average faces.

Recent studies have supported the link between averageness, heterozygosity (i.e. genetic diversity) and attractiveness. Heterozygosity in the major histocompatibility complex (MHC) genes that code for proteins involved in immune response, is positively associated with facial attractiveness [56] and facial averageness [57]. More directly, another study has shown that facial averageness is positively related to medical health as measured from actual medical records in both men and women [58]. Facial averageness can then be potentially associated with both direct benefits in terms of associating

with healthy, parasite- and/or disease-free partners and indirect benefits of heterozygous genes that can be passed onto offspring.

There is good evidence that average faces are indeed found attractive. Galton [59] first noted that multiple faces blended together were more attractive than the constituent faces. Recent studies have improved upon these techniques using computers to create digitally blended composite faces; generally, the more images in a composite, the more attractive it is found [60–62]. Aside from composite images, Light *et al.* [63] found that, in unmanipulated male faces, more attractive faces were rated as less distinctive, and Rhodes & Tremewan [64] found that higher averageness was associated with higher attractiveness when manipulating averageness via digital caricaturing.

Average faces are generally more symmetric and symmetry is typically attractive in faces (discussed in more detail above). Several studies have controlled for this confound in the original studies. When averageness and symmetry were independently manipulated, one study found that both manipulations positively and independently influenced attractiveness judgements [65]. Other studies have used perfectly symmetric images manipulated in averageness and still have demonstrated preferences for averageness [66,67]. Indeed, by comparing preferences for averageness when the effects of symmetry were controlled for and were not controlled for, Jones *et al.* [66] demonstrated that the contribution of symmetry to the attractiveness of average faces was minimal.

It has also been noted that, in the original composite studies, the more images that are blended together the smoother the skin texture becomes, as imperfections such as lines or blemishes are averaged [68]. Skin colour/texture has been controlled in studies that normalize the texture/colour of all the faces seen and all these studies demonstrate that average is attractive [62,64,66,67]. Examples of composite images and the effects of shape and colour averaging can be seen in figure 2.

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, facial averageness is also found attractive in Japanese participants [69] and in African hunter–gatherers [67].

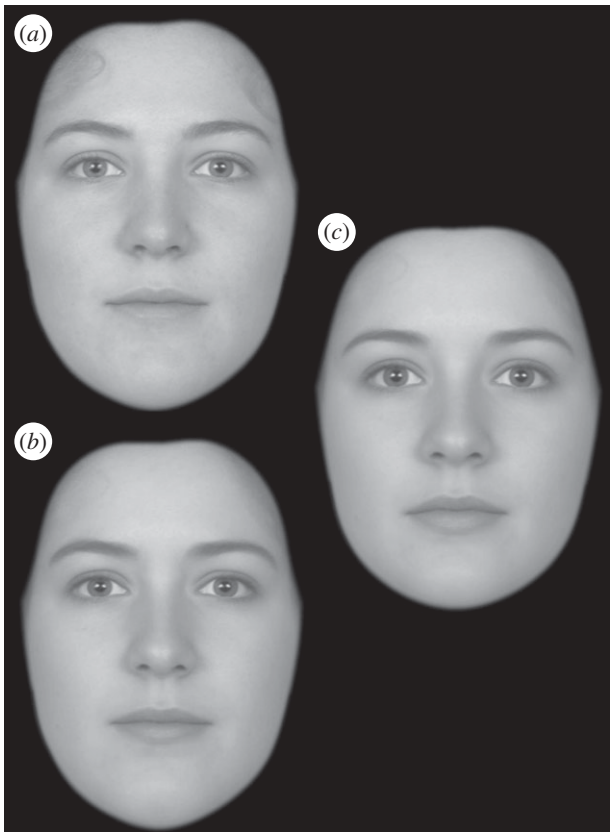

Figure 2. Averageness. (*a*) A composite image made from three images, (*b*) the same image given the colour of nine images and (*c*) a shape and colour composite made from nine images. Image (*c*) should be more attractive than both of the other images. Composites are made by marking key locations around the main facial features (e.g. points outline the eyes, nose and mouth) and the outline of each face (e.g. jaw line, hair line). The average location of each point of the component faces is then calculated to define the shape of the composite. The images of the individual faces are then warped to the relevant average shape before superimposing the images to produce a photographic quality composite image.

(c) *Secondary sexual characteristics in faces*

Male and female faces differ in their shape. Mature features in adult human faces reflect the masculinization or feminization of secondary sexual characteristics that occurs at puberty. These face shape differences, in part, arise because of the action of hormones such as testosterone. Larger jawbones, more prominent cheekbones and thinner cheeks are all features of male faces that differentiate them from female faces (e.g. [70]).

From an evolutionary view, extremes of secondary sexual characteristics (more feminine for women, more masculine for men) are proposed to be attractive because they advertise the quality of an individual in terms of heritable benefits; they indicate that the owners of such characteristics possess good genes. In other words, such traits advertise the possession of genes that are beneficial to offspring inheriting them in terms of survival or reproduction. One explanation of the importance of these facial traits is that they represent a handicap to an organism [71] and the costs of growing the trait means that only healthy individuals can afford to produce them. In this way, these 'honest' handicaps are proposed to indicate the fitness of the owner. For example, secondary sexual characteristics are proposed to be linked to parasite resistance because the sex hormones that influence their growth, particularly testosterone, lower immunocompetence. Testosterone has been linked to the suppression of immune function in many species [72], including humans [73,74]. Larger secondary sexual characteristics should be related to a healthier immune system because only healthy organisms can afford the high sex-hormone handicap on the immune system that is necessary to produce these characteristics [75].

In many non-human animal studies, there is a positive association between secondary sexual trait

expression and immunocompetence (e.g. [76]). The relationship between masculinity/femininity and good genes in humans is less clear. A study by Rhodes *et al.* [77], however, has shown that perceived masculinity correlated positively with actual measures of health in male adolescents. No relationship was found between femininity and actual health in female faces, though [77]. Another study has demonstrated that men's facial masculinity and women's facial femininity are negatively related to self reports of respiratory disease [35]. If health is heritable, then female preferences for masculinity and male preferences for femininity may indeed also reflect the choice of mates with good genes. There is also a link between hormonal profile and face shape. Women with higher circulating oestrogen have more feminine faces [78], while men with high testosterone have more masculine faces ([79], but see also [80]). If women with high oestrogen and men with high testosterone are valued as mates, preferences for cues of hormonal profile could drive preferences for sexually dimorphic face shape. Figure 3 shows faces manipulated in facial masculinity and femininity.

There is considerable evidence that feminine female faces are considered attractive. Studies measuring facial features from photographs of women [40,81,82] and studies manipulating facial composites [83] all indicate that feminine features increase the attractiveness of female faces across different cultures. If oestrogenized female faces provide cues to fertility and health, then male preferences for such features are potentially adaptive. This reasoning does not require oestrogen to be immunosuppressive or part of a handicap.

The link between masculinity and attractiveness in male faces is less clear. Cunningham *et al.* [84] and Grammer & Thornhill [40] used facial measurements and found that women preferred large jaws in men. 'Masculine' features, such as a large jaw and a prominent brow ridge are reliably associated with ratings of dominance in photographic, identikit and composite stimuli [83,85–88]. Despite some findings showing a preference for more masculine and dominant faces, several studies have shown that feminine characteristics and faces of low dominance are of increased attractiveness [62,83,84,89–91]. Many studies have made use of computer graphic techniques to manipulate masculinity. Sexual dimorphism in face shape can be manipulated by taking the geometrical differences between average male and female face shapes and applying this difference to new faces, making more or less masculine or feminine versions [83]. This process simultaneously changes all dimorphic shape characteristics in the face. For example, 'masculinizing' a male face shape by increasing facial proportions relative to the differences between a male and female average increases the size of the jaw and reduces lip thickness because male jaws are larger than female jaws and the lips of men are thinner than those of women. Perrett *et al.* [83] presented both Japanese and Caucasian faces in their country of origin. For the male face stimuli, the shape selected by Caucasians as most attractive was significantly feminized for both the Caucasian male face and the Japanese male face continua. Similarly, Japanese participants also selected significantly feminized versions of the male stimuli for both the Japanese and Caucasian male face continua. Thus, in both cultures it was found that participants showed a preference for feminized male faces. Since then, several studies have also documented preferences for femininity [62,90,92,93], but some similar computer graphic studies have also reported preferences for masculinity [94,95]. Although some of this variation may be attributed to other characteristics of the faces that varied between sets of stimuli [96], this does not explain the variability in preferences. We discuss the sources of individual differences in preferences for sexually dimorphic shape cues in the latter sections of our article.

Figure 3. Masculinity/femininity in faces. (*a*) Male and female composite images made more masculine and (*b*) more feminine. Masculinity is transformed using the difference between male and female face shape as defined by creating a male and female composite. Preferences for masculinity in male faces vary across studies, but feminine female faces are consistently found more attractive than masculine female faces.

(d) *Skin health and colour*

The face traits discussed so far have often been measured and manipulated but also studied in terms of perception and related to attractiveness. The reasoning for why traits like symmetry are preferred is often related to underlying health. Thus, it is important to examine perceptions of facial health directly. 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 (e.g. [44,97]). See figure 4 for examples of healthy and unhealthy appearing traits. In evolutionary terms,

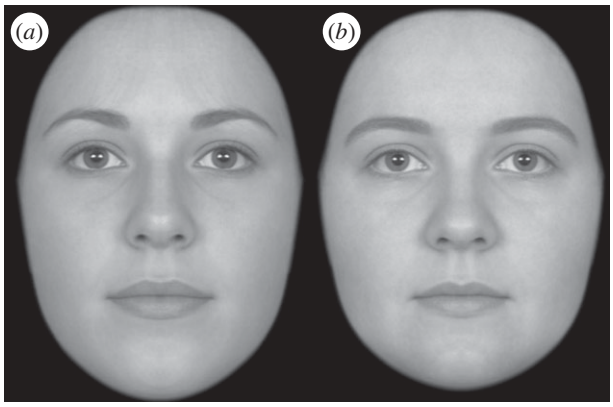

Figure 4. Facial healthiness. (*a*) Composite images of 15 women rated as high on healthiness and (*b*) 15 women rated as low on healthiness. High healthiness is associated with higher ratings of attractiveness.

there is a large and obvious selective advantage in detecting healthy partners both for social exchange and mate choice. Indeed, while the role of health in mate preferences is clear (see below), recent work has demonstrated that participants are more willing to reciprocate trust from healthy-looking social partners than from social partners who are relatively unhealthy-looking [98]. Such findings demonstrate the importance of health perceptions for social interaction generally. Again, as for previous traits, there may be both direct and indirect benefits to partnering with individuals who are perceived to be healthy.

There have been several studies that have addressed how facial appearance relates to the healthiness of an individual in humans. The three traits discussed above are often manipulated by changing only face shape, but health perception appears to be related to facial colour and texture also. Fewer studies have examined how colour and texture of faces influence attractiveness judgements. 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. Jones *et al.* [43] found that apparent health of facial skin is positively correlated with ratings of male facial attractiveness. In other research, homogeneity of skin colour was positively related to attractiveness [99]. Findings have also suggested that more heterozygous men also have healthier appearing skin [56]. Skin health may be a particularly useful marker of current health condition as it is more changeable than aspects such as symmetry or averageness.

Coloration is directly related to the appearance of skin. Coloration also appears to be an important component of sexual selection in many species. Red coloration is associated with dominance in fish [100], birds [101] and non-human primates [102,103] and, consequently, is linked to attracting the opposite sex. Recent evidence has suggested that primate trichromatic vision is an adaptation to distinguish colour modulations in skin based on blood flow, allowing assessment of the state and/or mood of conspecifics [104]. It has been noted that primates with trichromatic vision are generally bare-faced [104] and that, at least in humans, facial flushing is associated with anger and confrontation [105].

In research on non-human primates, there has been much interest in colour. For example, experimental manipulation of colour shows that female rhesus macaques prefer images of redder male faces [103], while males prefer images of redder female hindquarters [106]. In mandrills, red facial colour is related to rank in males [102], and females sexually present more frequently to brighter males and also groom them more frequently [107]. Red coloration also has consequences for behaviour in other species. For example, in bird species, the addition of red to stimuli can increase social dominance [108].

In humans, it has been shown that wearing red in a variety of physically competitive sports is associated with an increased chance of winning over opponents [109]. This has been interpreted as natural associations of red with dominance being extended to artificially displayed red in the same way that artificial stimuli can exploit innate responses to natural stimuli [108,110]. One study pitting red versus blue shapes found that red shapes were seen as more aggressive, dominant and more likely to win in physical competitions [111]. Red does generally seem to have aversive effects on human behaviour. For example, when taking exams, individuals move their body away from tests with red covers more than they do from those with green or grey covers [112]. While these studies suggest the colour red may be seen as a threatening stimulus in humans, 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 colours [113]. This effect appears to be specific to attractiveness judgements; red colour does not influence judgements of other traits such as kindness or intelligence and does not influence women's attractiveness judgements of other women [113]. Further research has examined red coloration in faces and demonstrated a positive association with perceived health [114]. The authors suggest that perception of healthy, oxygenated blood may drive associations between red and healthiness. Alongside redness, people also appear to think that skin yellowness is associated with healthy appearance in faces [114]. Yellowness may advertise health via an association with diet, as carotenoids are associated with skin yellowness and are absorbed via the intake of fruit and vegetables [114]. Taken together, these studies suggest that information on attractiveness and health is available from surface skin and that facial attractiveness is not dependent only on traits that display limited variation in adult life: skin texture and skin colour can vary over weeks or even days.

(e) *Facial cues associated with personality attribution*

In a classic social psychology study, Dion *et al.* [10] found that strangers rated attractive people as possessing 'socially desirable' traits to a greater extent than unattractive people, and that attractive people were also expected to lead better lives than unattractive

people. For example, attractive individuals were thought to be able to achieve more prestigious occupations, be more competent spouses with happier marriages and have better prospects for personal fulfilment. There has been a wealth of studies examining this attractiveness stereotype, demonstrating that attractive people are seen in a positive light for a wide range of attributes compared with unattractive people. On the basis of such studies, it has been suggested that there exists a stereotype associated with physical attractiveness, famously—'What is beautiful is good' [2] (see [11,12] for meta-analytical reviews of research on physical attractiveness stereotypes).

Studies on attractiveness stereotypes have generally not addressed the particular characteristics of faces that make individuals either attractive or unattractive, or the features that elicit personality attributions, although different faces reliably elicit the same personality attributions [115]. Expression certainly has large effects, with, for example, faces shown with smiles rated as more attractive and as having more positive personality traits than neutral faces (e.g. [116]). Such facial expressions are transient, however, and will differ rapidly within individuals over time and across photographs. Both baby-like and mature/dominant facial qualities are related and are more stable aspects of appearance that reliably elicit personality attributions cross-culturally (e.g. [88,117]), but their effect on attractiveness judgements, at least of men, is still in dispute, as noted earlier. Despite some findings showing a preference for more masculine and dominant male faces (e.g. [40]), several studies have shown that feminine characteristics and faces of low dominance are of increased attractiveness [84,89].

Personality traits are reported cross-culturally to be among the most important factors in partner choice by both sexes [1,118]. If desired personality is so important, it would appear likely that personality attributions elicited by a face would affect its attractiveness. For example, women who value cooperation and good parenting may avoid masculine-faced men. Thus, instead of feminine faces being attractive and this attractiveness driving positive personality attributions, it may be that the personality attributions are driving the attractiveness judgements.

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 (e.g. [119]), and so choosing a partner based on perceived personality may result in acquiring a partner who actually possesses desired personality traits. Attraction to faces based on personality stereotypes may happen regardless of whether attributions are accurate or not, especially as many individuals do believe that face provides an important guide to character [115,120]. In fact, it is possible that visually appearing to possess certain traits may be more important in initial selection processes than actually possessing desired traits because the visual stereotypes are more easily available than information about stable behaviour. One study has indeed demonstrated that a desire for some personality traits influences judgements of facial attractiveness [121]. 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, changing the result to: 'what is good is beautiful' [121]. 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 behavioural compatibility within couples, as people do tend to desire partners with personalities similar to their own [122].

One reason for variability in preferences for male facial masculinity may lie in the personality traits that masculine- and feminine-faced men 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 [83]. Cunningham *et al.* [84] have suggested that, because both masculine and feminine faces are only rated as moderately attractive, a resolution to this conflict could be that very attractive male faces possess a combination of factors and so reflect 'multiple motives' in female mate choice (i.e. the desire for a dominant and a cooperative partner, as advertised by a combination of masculine and feminine features). It appears then 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. Indeed, recent work has shown that masculine facial characteristics are associated with indices of physical dominance, such as physical strength [123], and the perception of such traits [124], and that feminine men show weaker preferences for short-term relationships and stronger preferences for committed, long-term relationships than their masculine peers do [125]. Feminization of male face shape may increase attractiveness because it 'softens' particular features that are perceived to be associated with negative personality traits. Women's face preferences may thus represent a trade-off between the desire for good genes and the desire for a cooperative partner. This trade-off means that masculinity may be more or less attractive under certain contexts and to certain individuals; we discuss this in §3.

(f) *Other traits and interactions*

Of course, the five types of trait listed above are not a complete list of factors involved in the judgement of facial attractiveness. Other face traits include factors such as age [126], weight/adiposity [127], hair and eye colour [128], facial hair in men [129] and make-up use in women [130]. Similarity to self also appears to be an influential trait and we review this factor in more detail in §3*b* as self-similar preferences vary according to social context [131,132].

While individual traits impact on attractiveness, there is also scope for interaction between them. We review

studies on interactions between emotion and attention in §3*b* as preferences for these traits also change according to social context. Certain face traits also appear to interact in generating preferences, however. For example, preferences for masculinity vary as a function of the healthiness of the face [96] and women's preferences for facial self-similarity are higher when men are more facially masculine [133]. Such interactions highlight that facial attractiveness judgements are not simple: many factors contribute to facial attractiveness and these factors can interact with one another.

3. ADAPTIVE INDIVIDUAL DIFFERENCES

In humans, while individuals may share certain basic criteria for finding faces attractive, many factors may influence the specific types of face they find attractive. In this section, we review three broad areas leading to individual differences in preferences: internal factors (e.g. hormonal state), context (e.g. mate-choice versus same-sex preferences) and exposure (e.g. visual experience).

(a) *Internal factors*

Research suggests that internal factors predict individual differences in several aspects of face perception, including attractiveness judgements. Importantly, the nature of these individual differences suggests adaptive design in face perception and face preferences. In the following section, we discuss two broad types of internal factors: (i) those related to hormone levels and fertility and (ii) those related to own condition, attractiveness and personality.

(i) *Hormone levels and fertility*

The influence of hormones on face perception is an area that has generated a considerable amount of empirical research in recent years. As detailed previously, masculine characteristics in men's faces are associated with measures of long-term medical health [35,77] and indices of developmental stability [36,37], physical strength [123] and reproductive potential [134]. By contrast, feminine characteristics in men's faces are associated with cues of investment and stronger preferences for long-term over short-term sexual relationships (e.g. [125]). There is now compelling evidence that how women resolve this trade off between the costs and benefits associated with choosing a masculine mate is affected by hormone levels and fertility.

Many studies have reported that women demonstrate stronger preferences for men displaying masculine facial characteristics around ovulation, when women are most fertile, than during other phases of the menstrual cycle [135–138]. Some studies have also reported that these cyclic shifts in women's preferences for masculine characteristics in men's faces are greatest among women who already have romantic partners and when women judge men's attractiveness for short-term, extra-pair relationships [138]. Although the ultimate function of these cyclic shifts remains somewhat controversial, many researchers have interpreted cyclic shifts in women's masculinity preferences as evidence for adaptations that function to increase offspring health via high paternal investment from a long-term partner while promoting attraction to other men displaying cues of heritable immunity to infectious disease when most fertile (discussed in [139]). Women may gain maximal benefits by selecting investing long-term partners and high-quality extra-pair partners. Importantly, other explanations that have been suggested, such as increased attraction to individuals who appear to be likely sources of high-quality care and support during phases of the menstrual cycle when increased progesterone prepares the body for pregnancy (i.e. the non-fertile, luteal phase), are not necessarily mutually exclusive with the more widely posited accounts that emphasize indirect benefits of women's mate choices (discussed in [140]). Increased attraction to masculine men is by no means unique to face preferences; women also demonstrate stronger attraction to masculine men when judging the attractiveness of men's voices [141–143], body shapes [144] and body odours [145], as well as when judging the attractiveness of videoclips of male behavioural displays of dominance [146,147]. Furthermore, converging evidence for fertility-related variation in women's preferences for facial masculinity comes from studies investigating circum-pubertal and circum-menopausal variation in women's masculinity preferences; post-menopausal and pre-pubertal women report weaker preferences for masculine facial characteristics than do their pre-menopausal and post-pubertal counterparts, respectively (e.g. [148,149]).

The ultimate function of cyclic shifts in women's preferences for masculine facial characteristics is not the only controversial aspect of cyclic shifts in women's masculinity preferences. For example, although some researchers have suggested that cyclic shifts in women's masculinity preferences may be an artefact of the computer graphic methods that are generally used in these studies to experimentally manipulate sexually dimorphic cues in digital face images [150], this claim is very difficult to reconcile with findings from studies that have demonstrated cyclic shifts in women's preferences for masculinity in real (i.e. unmanipulated) face images [151] and with the converging evidence for cyclic shifts in women's preferences for masculinity from studies that have assessed preferences for masculinity in other domains (e.g. behaviour, personality descriptions, body odour) and that did not use computer graphics to prepare their stimuli (e.g. [146,147]). While these findings suggest that cyclic shifts in women's masculinity preferences are not an artefact of the stimuli used, an aspect of research on cyclic shifts in women's masculinity preferences that remains controversial is whether the effect of cycle phase on women's face preferences is relatively specific to judgements of men's faces, or also occurs when women judge the attractiveness of other women. To date, evidence is equivocal; some studies have observed cyclic shifts in women's preferences for masculine-faced men, but not masculine-faced women [135], while others have observed cyclic shifts in women's preferences for masculine faces, irrespective of their sex [136,152]. These latter papers speculate that cyclic

shifts in women's preferences for masculine-faced women could represent a low-cost functionless by-product of a mechanism that evolved primarily to increase women's preferences for masculine men around ovulation [136], or have suggested that higher attractiveness ratings given to masculine women around ovulation could reflect increased derogation of feminine, and therefore attractive, same-sex competitors when women are most fertile [152] (see also [149]).

In addition to the sex-specificity of the effects of cycle phase on face preferences, the mechanisms that underpin cyclic shifts in women's preferences for masculine characteristics in men's faces have also been a topic of considerable interest in recent years. For example, research into the hormonal mechanisms that might underpin these cyclic shifts has variously emphasized the effects of variation in levels of testosterone [152], oestrogen [153] and progesterone [136,141], or has suggested, perhaps unsurprisingly, that cyclic shifts in women's masculinity preferences might be best explained by complex interactions among multiple hormones [142,152]. While findings from research into the hormonal mechanisms that might underpin cyclic shifts in women's masculinity preferences have arguably been inconsistent, the findings of corresponding research into the psychological mechanisms have been relatively consistent; various studies have demonstrated that women are quicker to categorize men and access male stereotypes around ovulation (e.g. [154,155]) or have suggested that women's preferences for masculine men are correlated with their level of sexual desire [156,157]. These findings suggest that cyclic variations in stereotype access and sexual desire might be important psychological mechanisms for regulating facial masculinity preferences during the menstrual cycle.

While research on hormone-mediated face perception has generally focused on women's judgements of men's attractiveness, some recent research has investigated hormone-mediated face preferences among men. Men, of course, do not cycle in the same way women do, but levels of testosterone fluctuate within individuals. Research using natural variation in testosterone has shown that men's preferences for feminine characteristics in women's faces are stronger when their testosterone levels are high than when they are relatively low [158]. This finding suggests that hormones, such as testosterone, can generate within-participant individual differences in face preference in men.

As can be seen from the previous paragraphs, there is compelling evidence that women's preferences for masculine men, be they assessed from face preferences or from preferences for male characteristics in other domains, vary systematically over the menstrual cycle. Whether or not preferences for other putative cues of men's long-term health are similarly affected by menstrual cycle is equivocal, however. For example, although many studies have demonstrated that women's preferences for the body odours of symmetric men are enhanced around ovulation (reviewed in [139]), evidence for cyclic shifts in women's preferences for symmetry in men's faces is inconsistent. One study has found that women's preferences for symmetric male faces were stronger around ovulation than during other phases of the menstrual cycle, at least among partnered women who were instructed to judge men's attractiveness as short-term mates [159]. By contrast, other studies have observed no evidence for cyclic shifts in women's preferences for symmetric men's faces (e.g. [150]), although one study with a null finding for preference did find that women's ability to detect asymmetries in men's faces varied over the menstrual cycle in the predicted manner [160]. Given that women's preferences for symmetry and masculinity in men's faces are correlated across individuals [161], suggesting that facial masculinity and symmetry signal some shared information and that women respond to them in similar ways, the inconsistent effects of cycle phase on women's preferences for facial symmetry are rather surprising.

Although evidence that women's preferences for symmetry in men's faces vary systematically over the menstrual cycle is equivocal, that is not to say that robust cyclic shifts in women's perceptions of faces are only evident in their preferences for facial masculinity. For example, women's aversions to self-resembling faces are enhanced around ovulation and positively correlated with women's estimated progesterone levels during the menstrual cycle [162]. This variation in attitudes to self-resembling faces may reflect increased inbreeding avoidance around ovulation and increased preferences for caring, supportive and trustworthy individuals when increased progesterone prepares the body for pregnancy [163]. Moreover, women's aversions to facial cues associated with current illness (e.g. pallor) are also greater when increased progesterone level prepares the body for pregnancy, potentially reflecting mechanisms to compensate for maternal immunosupression during the early stages of pregnancy and helping to maintain normal foetal development [97,136]. Indeed, pregnant women and women using oral contraceptives which mimic the effects of increased progesterone during pregnancy demonstrate stronger aversions to individuals displaying facial cues of illness than do women with natural menstrual cycles [97]. These latter findings for aversions to facial cues of illness and progesterone during the menstrual cycle complement other research on increased aversions to possible sources of contagion in women's food preferences during pregnancy [164], as well as increased sensitivity to facial expressions signalling that sources of threat and contagion are nearby when progesterone levels are raised [165,166].

While our discussion of hormone-mediated face preferences in women has emphasized the positive findings that have been reported in the literature, it is important to note that there have also been unsuccessful replications of cyclic variation in women's face preferences. For example, two recent studies observed no evidence for cyclic variations in women's preferences for masculine versus feminine male faces [150,167]. One possible explanation of these null findings comes from findings that suggest the extent to which women's preferences for masculine men vary

over the menstrual cycle vary systematically among women. For example, cyclic variation in women's preferences for masculine characteristics in men's voices is significantly greater among women with high trait (i.e. average) oestrogen levels than it is among women with relatively low trait oestrogen levels [142]. This pattern of results may occur because varying their sexual strategy during the menstrual cycle may benefit unattractive women more than it benefits attractive women [142]. More recent research has presented additional evidence that women's family background, prenatal hormone levels and mortality salience might also affect the extent to which they vary their masculinity preferences according to their menstrual cycle phase [168–170]. We also note that there are significant methodological differences between studies examining cycle effects, making direct comparisons (e.g. between those reporting null and positive effects) difficult. For example, some studies distinguish between short- and long-term mating contexts, generally with larger cyclic shifts for short-term judgements [139], while others do not [167]. Studies also differ in stimuli number, stimuli type and how fertility is defined. A thorough description of methodological differences between studies is not the focus here, but methodology is certainly a factor that could explain differences in findings across studies. It is likely that further research concerning individual differences in cyclic shifts and comparing different methodologies would provide important insights into the motivations, functions and mechanisms behind cyclic shifts in fundamental aspects of face perception.

(ii) *Own condition, attractiveness and personality*

While the previous section discussed research implicating hormone levels and fertility in individual differences in face perception, this section will discuss the relationships between face preferences and indices of own condition and attractiveness.

Several studies have reported positive correlations between women's ratings of their own physical attractiveness and the strength of their preferences for masculine characteristics in men's faces [92]. Other studies have extended this work by demonstrating that more objective measures of women's condition and attractiveness, such as their waist–hip ratio or oestrogen levels, predict their preferences for masculine characteristics in men's faces in the same way [171,172]. Similar correlations between indices of women's own attractiveness and the strength of their preferences for masculine characteristics in other domains, such as men's voices, have also been reported [173,174], and indices of women's own condition and attractiveness are positively correlated with the strength of their preferences for symmetry and healthy-looking skin in men's faces [92,175].

The findings described above appear to be somewhat analogous to condition-dependent preferences observed in other species, in which individuals in good physical condition show stronger preferences for high-quality mates (e.g. [176]). Condition-dependent preferences in both humans and non-humans may have a common function and occur because individuals in good physical condition (i.e. attractive individuals) are better able to compete for and/or retain high-quality mates [92]. Particularly compelling evidence for this proposal comes from one of the few experimental studies of condition-dependent mate preferences. Little & Mannion [95] showed that women who viewed a slideshow of highly attractive women reported lower self-rated attractiveness and demonstrated weaker preferences for masculine characteristics in men's faces than did women who viewed a slideshow of relatively unattractive women. These findings suggest that women recalibrate subjective impressions of their own attractiveness (i.e. impressions of their own 'market value') according to their recent experience with same-sex competitors and that this, in turn, leads to a recalibration of their mate preferences. While early work on the role of own attractiveness in mate preferences emphasized the importance of the judge's own health, Little & Mannion's findings suggest that condition-dependent preferences might be more usefully conceptualized as 'market value dependent preferences'.

While the research described above focused on the relationships between mate preferences and both individuals' own physical characteristics and their subjective evaluations of these physical characteristics, other work on condition-dependent preferences has investigated whether personality traits and other psychological factors predict individual differences in mate preferences in similar ways. For example, individual differences in systemizing and sensation-seeking, both of which are components of male sex-typical psychology, are positively correlated with men's preferences for feminine characteristics in women's, but not men's, faces [177,178]. Among women, individual differences in empathy, a component of female sex-typical psychology, and extraversion, a key predictor of social status that is correlated with women's physical attractiveness, are positively correlated with preferences for masculine characteristics in men's, but not women's, faces [177,179]. These findings not only implicate personality traits in individual differences in face preferences but also raise the intriguing possibility that some personality traits might mediate the relationships between an individual's physical characteristics and their face preferences.

(b) *Context*

While factors such as hormones and own attractiveness can explain differences in face preferences between individuals, the context under which judgements are made can also contribute to variation in standards of beauty. In the following section, we discuss how context affects face preferences in three types of contexts: (i) social contexts, such as when judging potential mates versus potential cooperative partners; (ii) temporal contexts, such as long- versus short-term relationships; and (iii) environmental contexts, such as environments with high versus low pathogen load.

(i) *Social context*

Information about genetic kinship is available in the face and is perceived somewhat accurately [180–184].

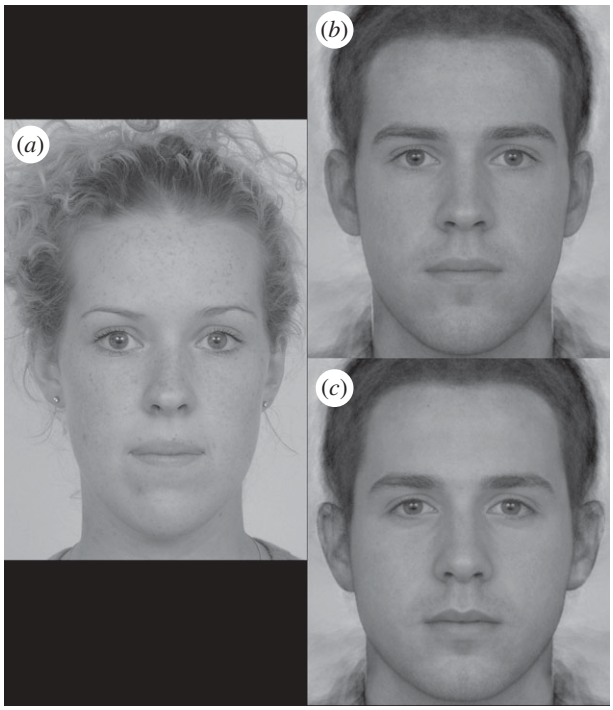

Figure 5. Transforms of self-similarity. (*a*) Original picture, (*b*) self-similar and (*c*) self-dissimilar opposite-sex images. Images are made by using the difference between a composite image of the same sex and an individual participant to make faces more similar to the participant. Self-dissimilar faces can be made by applying the same technique but using images other than the participant.

Judgements of facial similarity are highly synonymous with judgements of kinship [185–187], and facial similarity produced by computer-graphic manipulation affects behaviour in ways consistent with inclusive fitness theory (e.g. increasing cooperation in economic games; [188,189]). Therefore, responses to facial resemblance are likely to be affected by prosocial versus sexual contexts.

Cues of kinship are predicted to increase preferences in non-sexual, prosocial contexts, owing to the benefits associated with inclusive fitness [190]. In other words, evolutionary models show that behaviours that benefit other individuals who share genes through common descent will be favoured. Therefore, if physical similarity is a reliable cue of genetic relatedness, we expect individuals to act prosocially towards individuals who appear similar to themselves. However, cues of kinship should have a less positive effect in sexual contexts, because of inbreeding's detrimental effects on offspring quality [191]. One study investigated this prediction by comparing perceptions of the attractiveness of self-resembling own-sex and opposite-sex faces [131]. Male and female 'siblings' of both male and female participants were manufactured using computer-graphic methods detailed in DeBruine *et al.* [163]. Participants judged self-resemblance to be more attractive in the context of own-sex faces than in the context of opposite-sex faces. However, there was no such opposite-sex bias when the same faces were judged for averageness. This own-sex bias in preferences for self-resemblance indicates that, while self-resemblance is attractive in an exclusively prosocial (i.e. nonsexual) context, it is less attractive in a potential mating context. Stronger attraction to cues of kinship in own-sex faces than in opposite-sex faces is likely to promote prosocial behaviour towards own-sex kin, while minimizing occurrences of inbreeding with opposite-sex kin. Examples of manipulations of self-similarity can be seen in figure 5.

Further evidence for context sensitivity in judgements of self-resembling faces is provided by a study comparing men's and women's preferences for self-resemblance in opposite-sex faces in explicitly prosocial versus sexual contexts [132]. Participants were shown images of self-resembling opposite-sex faces and asked to judge their trustworthiness (i.e. prosocial context), attractiveness for a short-term relationship (i.e. sexual context) and attractiveness for a long-term relationship (i.e. both prosocial and sexual context). Consistent with both inclusive fitness and inbreeding avoidance theories, self-resemblance increased perceptions of trustworthiness, decreased attractiveness for short-term relationships and had no significant effect on attractiveness for long-term relationships. The fact that self-resemblance in opposite-sex faces was found to be trustworthy, but not attractive in short-term contexts, emphasizes the context-sensitivity of responses to self-resemblance. Importantly, because familiarity increases judgements of both attractiveness and trustworthiness [192], this pattern of context-sensitivity strongly suggests that responses to self-resemblance do not occur simply because of familiarity alone (i.e. the mere exposure effect [193]).

Another example of social context influencing face preferences comes from research on interactions among the effects of different facial characteristics on preferences. For example, both behavioural and neurobiological evidence suggest that viewers demonstrate stronger attraction to attractive physical cues in faces (e.g. attractive face shapes or attractive colour) when viewing faces demonstrating positive social interest in the viewer than when viewing faces that appear uninterested in the viewer (e.g. [194,195]). Similarly, behavioural and neurobiological evidence also suggests that viewers demonstrate stronger attraction to cues associated with positive social interest (e.g. eye contact and perceiver-directed smiles) when viewing physically attractive individuals than when viewing relatively unattractive individuals (e.g. [196–199]). Such findings may reflect mechanisms for efficient allocation of mating and/or social effort and can be further modulated by social context. Conway *et al.* [196], for example, found that men and women showed stronger preferences for perceiver-directed smiles from opposite-sex than own-sex individuals when judging others' attractiveness, but not when judging their likeability.

(ii) *Temporal context*

The trade-off theory of women's masculinity preferences proposes that contextual factors that alter the relative importance of the benefits and costs associated with choosing a masculine partner (see §2*c* above) will affect the strength of women's preferences for masculine versus feminine men [25,83,92,93,138,200–202].

For example, women can only make use of the benefit of genetic health for offspring when they are able to conceive and, as discussed above (§3*a*(i)), women's preferences for masculine men are modulated by their fertility. Similarly, the putative costs of low investment are much less of a concern in short-term than in long-term relationships and, thus, women may demonstrate stronger masculinity preferences when judging men's attractiveness as possible short-term than long-term partners.

Little *et al.* [93] tested this prediction by measuring women's masculinity preferences separately in the context of a short-term and a long-term relationship. Participants interactively manipulated a male face along a continuum from 50 per cent feminized to 50 per cent masculinized until it was 'closest to the appearance you would find attractive for a short- (or long-) term relationship'. Women who were not using oral contraceptives made this face more masculine in the context of a short-term relationship than in the context of a long-term relationship.

Penton-Voak *et al.* [203] also found that women preferred slightly more masculine faces in the context of a short-term relationship than in the context of a long-term relationship, and that this pattern was exaggerated in the least attractive participants (i.e. women with high waist–hip ratios or low other-rated facial attractiveness). One potential explanation for this pattern of preference is that attractive women are better able to compete for, retain or replace high-quality, masculine partners and, therefore, do not show as large a shift in their preferences between short-term and long-term contexts. Indeed, several studies have shown that more attractive women show stronger preferences for masculine faces and voices (reviewed above in §3*a*(ii)).

The effects of temporal context on judgements of attractiveness are not limited to faces. Women prefer lower pitched male voices in the context of a short-term relationship than in the context of a long-term relationship [143]. This same study also found that the effect of relationship context was greatest when women were in the fertile phase of the menstrual cycle, a finding that is consistent with research on cyclic shifts in preferences for facial masculinity [138].

(iii) *Environmental context*

A strong theoretical prediction of the trade-off account of variability in women's preferences for masculine men is that women in environments where poor health is particularly harmful to survival (e.g. environments with high prevalence of pathogens and inaccessible or poor healthcare) will demonstrate stronger preferences for cues of health [25,83,92,93,138,200–202]. Regional differences in pathogen prevalence have been shown to be positively correlated with the importance placed on physical beauty and health [204,205].

DeBruine *et al.* [206] investigated the relationship between environmental cues of the importance of health and women's preferences for masculinity in a sample of 30 countries. Health statistics from the World Health Organization were used to compute a 'national health index' (NHI), which was negatively correlated ($r = -0.62$) with women's average masculinity preferences for each country. This relationship remained significant, even when controlling for regional variation in wealth and women's mating strategies (i.e. whether women tended to pursue more short-term or long-term relationships; [207]).

Brooks *et al.* [208] have re-analysed these data and suggested that regional variation in women's masculinity preferences may be better explained by regional variation in male–male violence. Masculine-faced men may be favoured under such conditions, for example, as they may be better able to compete for resources. A further study of US states, in contrast, has shown that environmental health factors, and not indices of male–male violence such as homicide rates, predicts regional variation in women's masculinity preferences [209]. Health, wealth and male–male violence are, of course, inter-related. While it is ultimately possible that health, wealth and male–male violence may all individually contribute to variation in preference, it is important to note that all of these analyses show that regional variation in women's masculinity preferences occurs in ways that are highly consistent with trade-off theories of sexual selection.

The availability of resources in an environment may also influence face preferences. In low-resource environments, the resources to raise a child may be scarce or difficult to acquire and a preference for an investing partner be adaptive. In contrast, in higher resource environments, there may be little gain in terms of offspring survival and reproduction by the additional effort of a second parent and a preference for 'good genes' may be a better strategy [210,211]. To test these ideas, Little *et al.* [212] tested men's and women's preferences for masculinity/femininity in two contexts: a harsh environment with few resources and a safe environment with plentiful resources. Both men and women decreased their preferences for high quality mates for long-term relationships in the context of a harsh environment. For example, women were relatively more attracted to feminine faced men for long-term relationships in low resource environments, suggesting that women value potential investment from these men more than the higher dominance/health of masculine faced men under these conditions. This is consistent with the logic of trading genetic quality for commitment and investment in environments where resources are scarce.

(c) *Visual experience*

Individuals are confronted with a myriad of faces and social interactions every day. Research has shown that such experience leads to changes in preferences for faces. In the following section, we discuss two aspects of visual experience examining: (i) how exposure can impact on preferences and (ii) how observing the choices of others may affect our preferences.

(i) *Exposure*

Familiarity is a powerful determinant of attraction. For many types of stimuli, including faces, exposure

increases attraction even when the exposure is unconscious [213–215]. Structural features of the face must be stored and represented in order to determine familiarity. As noted earlier, one idea for why averageness in faces is attractive comes from a link with familiarity—as average faces appear familiar this could positively affect their attractiveness [60,62].

Familiarity, when not paired with aversive stimuli, is thought to be rewarding [214], and indeed there are obvious benefits to avoiding the unfamiliar. This can then help explain why exposure may cause increases in preference. There may, however, be more to increasing face preference than simple exposure. For example, recent studies have demonstrated that the nature of association (positive or negative) can affect face preferences, with positive experiences leading to increased attraction and negative experiences to decreased attraction [216]. Moreover, these effects of valenced exposure are not bound solely to the specific individuals who were encountered and generalize to judgements of novel, physically similar individuals [216].

Familiarity with parental traits has been implicated in human preferences. The phenomenon of imprinting, whereby individuals are attracted to parental traits, is well-studied in non-human animals [217,218] and there is increasing evidence for similar effects in humans. Following studies of facial similarity, judges have been shown to correctly match wives to their mother-in-law at a significantly higher rate than expected by chance and that wife–mother-in-law similarity is higher than similarity between husbands and their wives [219]. Such effects are also seen in adopted daughters, controlling for any potential genetic effects, with significant facial resemblance between daughter's husband and her adoptive father [220]. Other studies have shown that, for hair and eye colour, the best predictors of partner traits are the opposite-sex parent's colour traits [128] and that individuals are attracted to age in faces consistent with the age of their parents when they were born [221]. It is worth noting that at least in one study, effects were seen mainly for the opposite-sex parent [128], which may indicate a more complex mechanism than simple exposure. Another line of argument suggesting imprinting-like effects appear not simply to reflect exposure comes from studies that have shown effects to be dependent on the quality of the relationship to the parent [220,222]. For example, daughters who report that they received greater emotional support from their adoptive fathers are more likely to choose mates who are similar to their father than individuals who report their father provided less emotional support [220]. Similarly, women who rate their childhood relationships with their father positively show stronger attraction to face proportions similar to their father's face than women who rate their relationships less well [222]. Imprinting-like effects then appear more complicated than simple exposure being directed more to one parent than the other and showing dependence on the relationship with that parent.

Imprinting-like effects may lead to positive assortative mating (pairing with similar partners), at least for long-term relationships, and this may have benefits in terms of keeping adaptive suites of genes together [223] or increasing behaviour compatibility [224]. There is certainly evidence that couples resemble each other facially [225,226]. While there are costs to inbreeding, as discussed earlier, a certain amount of genetic similarity can be beneficial—so-called 'optimal-outbreeding' [227]. Potentially then, a system that learns about known individuals and increases attraction to their face traits could be adaptive.

Both familiarity and imprinting posit that exposure affects attractiveness. In recent years, exposure has been thought to have specific effects on our representations of faces via visual adaptation. We are unlikely to have an inbuilt average face and what is average must be calculated from experience. For each class of stimuli, the human visual system encounters may develop an individual representation, or prototype, made up of an average of the characteristics of all the different stimuli of that type that have been seen [228–232]. Computer modelling has revealed that algorithms trained to discriminate different stimuli produce stronger responses to stimuli that represent the average of the training set, even though this average was not previously encountered [228,230]. These findings have been interpreted as evidence that prototype formation is a property of learning to recognize different stimuli as members of a class [228,230].

Studies on category learning have a long history (e.g. [233]). Learning studies examine how categorical perception develops using abstract stimuli. In classic studies, it has been shown that exposure to different dot patterns with particular configurations results in abstraction so that the average of each of the patterns, while never previously seen, is recognized as belonging to the set of patterns from which it was derived [233].

Faces have been the focus of much research regarding recognition and prototype formation. While it has been proposed that faces may be coded as veridical representations of individuals or exemplars [232], recent neuroimaging and single-cell recording studies have supported a prototype-referenced model of face coding [229,231]. Exposure to faces biases subsequent perceptions of novel faces, causing faces similar to those initially viewed to appear more prototypical than they would otherwise be perceived as, presumably, a prototype or population of exemplars becomes updated [234–239]. For example, adaptation to faces with contracted features causes novel faces with contracted features to be perceived as more normal than prior to this exposure [235,239,240]. Analogous visual after-effects have been observed following exposure to faces varying in identity [234,236], ethnicity [237], sex [235,237,241], expression [237], mouth shapes associated with different spoken sounds [242] and masculinity/femininity [192,243]. Such after-effects are thought to reflect changes in the responses of neural mechanisms underlying face processing [235,238–240].

These studies may then shed light on how the brain builds an average representation to which the other faces can be compared. Importantly, exposure in the manner described above also influences attractiveness judgements. After exposure to faces possessing certain traits, these traits come to be preferred

[192,240,243,244]. For example, if exposed to faces that look more like one identity, then new faces that resemble that identity are found more attractive than if exposed to the opposite set of face traits. A similar effect has also been observed for judgements of the trustworthiness of faces [192]. Adaptation then reflects the rapid updating of face norms and can therefore be tied both to the effects of familiarity and imprinting-like effects.

(ii) *Social learning*

We have dealt briefly with some aspects of simple experience on preferences above, but, of course, humans are highly social and much human experience is of what other humans do. Humans can therefore learn about attractiveness from the behaviour of those around them: social learning of preference. We have recently reviewed social learning in human face preferences [245], and so present a brief overview here.

Individuals often learn from others and selection for social learning mechanisms may occur when there are costs to acquiring accurate behavioural information via individual learning [246]. Social learning can be adaptive if it allows an individual to assess potential mates more quickly and efficiently than through individual trial and error or allows an individual to use another's expertise. Mate choice copying has been observed among females in a number of different non-human species [247–250], including fish [251–254] and bird species [255–257]. Such studies have generally shown that when females observe another female (the model) to be paired with one of the two males (the targets), they are subsequently more likely to prefer the target male they had seen paired with the model over the male that was not paired with the model.

Inspired by work on non-human species, recent research also suggests that social learning may influence human mate preferences. While some research has shown that the presence of wedding rings on men did not increase women's preferences for those men [258], other studies have found that images of men labelled as married were more attractive than those labelled as single [259] and that women rate men as more desirable when they are shown surrounded by women than when they are shown alone or with other men [260]. Another study has shown that women prefer pictures of men that had been previously seen paired with images of other women who were looking at the face with smiling (i.e. positive) expressions compared with pictures of men who had been seen paired with images of women with neutral (i.e. relatively negative) expressions [261]. Women therefore do appear to mimic the attitude of other women to particular men.

Alongside partnership status, simple presence, and expressions of attitude towards the male, the physical traits of the observed model may also play a role in the social transmission of preference. Previous studies have shown that men's and women's attractiveness judgements are influenced by the apparent choice of attractive members of the same sex. Sigall & Landy [262] used real individuals to show that positive characteristics are attributed more frequently to men who are paired with attractive rather than unattractive women. In this way, they show that an attractive partner may 'radiate beauty'. Such a phenomenon suggests a more sophisticated form of mate-choice copying, whereby women can use the attractiveness of a partner that a man can acquire in order to judge the man's own attractiveness. Another study using images that were presented with a fictitious partner has shown that both men and women find a face paired with an attractive partner to be more attractive than one paired with an unattractive partner for a long-term but not a short-term relationship [263]. Effects specific to long-term preferences in humans suggest that social information is being used to infer non-physical traits that make a target a good long-term partner, such as resources or intelligence, which may be difficult to determine from physical appearance alone.

4. SUMMARY AND CONCLUSIONS

Being more or less attractive has important social consequences and people do generally agree on who is and who is not attractive. Beauty is not just a simple social construct—attractiveness appears to be ingrained in our biology. While some aspects of face perception might be innate, other aspects are clearly influenced by experience; it seems unlikely that individuals are born with a representation of what a perfect partner looks like.

Structural and other aspects of human facial appearance are linked to preferences (§2). If a trait reliably advertises some benefit to the perceiver, then we would expect individuals in a population to find that trait attractive. It is clear that individual differences in preferences for some traits will prove adaptive and so are consistent with evolutionary theory. We document several potentially adaptive individual differences in human face preferences as well as other factors that may lead to variable preferences (§3). Research on human facial attractiveness has benefited greatly from an evolutionary/biological perspective, both in terms of documenting what traits are likely to be important and in predicting individual variation. Work on facial attractiveness is also integrative, combining theories and methods from behavioural ecology, cognition, cross-cultural research and social psychology.

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