Facial attractiveness

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Humans in societies around the world discriminate between potential mates on the basis of attractiveness in ways that can dramatically affect their lives. From an evolutionary perspective, a reasonable working hypothesis is that the psychological mechanisms underlying attractiveness judgments are adaptations that have evolved in the service of choosing a mate so as to increase gene propagation throughout evolutionary history. The main hypothesis that has directed evolutionary psychology research into facial attractiveness is that these judgments reflect information about what can be broadly defined as an individual's health. This has been investigated by examining whether attractiveness judgments show special design for detecting cues that allow us to make assessments of overall phenotypic condition. This review examines the three major lines of research that have been pursued in order to answer the question of whether attractiveness reflects non-obvious indicators of phenotypic condition. These are studies that have examined facial symmetry, averageness, and secondary sex characteristics as hormone markers.

The view that physical beauty is arbitrary, whimsical and unrelated to biological function has characterized much of the social scientific study of attractiveness and social commentary on the topic[1]. Evolutionary theory provides reasons to be very skeptical of this view. Like other species, humans have an evolutionary history during which selection-guided phenotypic and genotypic changes occurred[2–5]. Although selection is not the only cause of evolution, it *is* the only cause of adaptations. Like the rest of the body, the human brain is the result of multiple adaptations, solutions to problems that influenced the reproductive success (RS) of individuals over the evolutionary history of the species. One such problem was obtaining a mate who would promote one's own genetic survival by reproducing successfully. Selection should have favored psychological features that (1) evaluated observable bodily traits that varied with mate value (what an individual brings to a relationship that affects the partner's RS), and (2) found attractive those traits connoting high mate value. Selection favors functionally specific adaptations rather than general-purpose ones, because only specialized mechanisms can solve the specific problems that are the forces of selection (e.g. obtaining a mate who has genes that promote offspring survival). When members of a species discriminate between potential mates with regard to their physical appearance, as humans do, a reasonable working hypothesis is that the discrimination reflects special-purpose adaptations responsive to cues that had mate value in evolutionary history[6]. Recent evidence provides considerable support for this working hypothesis.

Attractiveness as a health certificate

Facial attractiveness assessments are more similar than different across sexes and sexual orientations, ethnic groups, and ages from infants to the elderly[7–12], with correlations between two raters' judgments typically in the range 0.3–0.5. Even within and between human groups with little or no contact with Western standards of beauty, there is appreciable agreement in facial attractiveness ratings[11]. Naturally, different societies do not place precisely the same value on all traits (and, as we indicate below, should not be expected to do so from an evolutionary perspective). However, the fact that humans share views about what features are attractive suggests that there are species-typical psychological adaptations.

Evolutionary psychologists studying physical attraction and attractiveness have been inspired by Donald Symons's book, *The Evolution of Human Sexuality*, which presented evidence that human attractiveness evolved because of mate preference for healthy and fertile mates[13]. Evenly colored, smooth, pliant skin, clear eyes and shiny hair are viewed as attractive, as well as signs of being disease-free. In its broadest sense, however, health status is not merely the presence or absence of disease. Rather, it can be defined as 'phenotypic condition' – the ability to acquire and allocate resources efficiently and effectively to activities that enhance survival and reproduction (i.e. the ability to garner and convert energy into returns in evolutionary fitness). By this view, two pathogen-free individuals who differ in metabolic efficiency (and, therefore, the fitness returns on energy expenditure) differ in health status. Moreover, two individuals who differ in their ability to accrue and allocate energy effectively might allocate similar resources to immune function and have similar rates of disease, yet one could have a greater ability to convert energy into fitness returns and, therefore, have better phenotypic condition (everything else being equal). Overall condition can be affected by a number of factors, including mutations, pathogens, toxins and other insults experienced during development. Because mutations and the ability to resist pathogens and toxins can be heritable, overall phenotypic condition is also expected to be partly heritable.

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Assessments of the phenotypic condition of others probably affected individual RS in all types of social alliances during human evolutionary history, not just mate choices[2]. Accordingly, attractiveness assessments could reveal information about an individual's phenotypic condition that matter in terms of decisions about nepotistic investment (e.g. whether to invest parental care in a particular offspring; attractive and healthy children receive more parental care[2,10,14]) and decisions about reciprocity. The term reciprocity refers to the consequences of one's choice of friends and other nonmate social allies – unhealthy allies might not survive to reciprocate one's aid[2]. Physical attractiveness shows consistency across the life cycle from childhood through to adulthood[12,15,16] and, therefore, attractiveness at any age potentially predicts health at later ages. As is expected from this view, the prediction that attractive people of all ages receive favorable treatment from others is upheld by the available evidence[10,12,17,18].

The hypothesis that beauty is associated with health has been examined in a number of studies. In one recent large study, men's and women's attractiveness assessed during the teenage years was compared with health assessed years later[19] and no relationship was found. In another study, the results weakly supported a relationship[20]. Although these findings might appear to be damaging to the view that attractiveness perceptions have evolved as assessments of health, they are, in fact, not directly relevant. Firstly, the concept of health status considered here is a broad one, as noted above, not merely disease incidence. Secondly, this perspective predicts that attractiveness should have been related to phenotypic condition in environments of evolutionary adaptedness (EEA) – the evolutionary environments over the last several million years that were the selective forces that ultimately caused human-specific adaptations[21–23]. Because modern humans live in environments replete with evolutionary novelty (e.g. modern contraception, modern medicine and middle-aged women who appear nubile because of nulliparity), facial attractiveness and male and female RS might not be associated to the same extent as previously.

How, then, can scientists assess the hypothesis that attractiveness evolved as an assessment of phenotypic condition? One strategy is to examine health in human environments that are most similar to the EEA. In the Ache Indians of Paraguay, a hunter-gatherer society, Hill and Hurtado[24] found that facially attractive women have 1.2 times the fertility of women with average attractiveness (with age-controlled groups). Interpretation of this result requires further investigation, as the impact of attractiveness on mating might have affected fertility; thus, this relationship might not be a result of an association between health and attractiveness. The fact that, across many countries, attractiveness is most important as a mate-choice criterion in areas where parasites are most prevalent[25] is also consistent with attractiveness being a health certificate, but is indirect evidence.

A second and more powerful strategy is to take an adaptationist approach. The adaptationist attempts to answer questions of the form 'what is the function of this feature?' by a process of reverse engineering[22,26,27]. Features that qualify as adaptations tend to exhibit special design. They possess elements that render them effective solutions to specific adaptive problems. Reverse engineering shows that a feature possesses special design as a solution for a particular adaptive problem. Special design not only provides evidence that the feature is an adaptation but also evidence of what the feature is an adaptation for. To assess the hypothesis that facial attractiveness judgments evolved as assessments of overall phenotypic condition, the adaptationist asks whether these judgments possess elements revealing that they would have functioned as assessments of overall phenotypic condition in historical environments.

Box 1. Other approaches to the study of facial symmetry

Four early experimental studies (Refs a–d) examined attractiveness ratings of symmetrical faces created by aligning a hemi-face with its mirror reflection. [Mealey *et al.* (Ref. e) used hemi-face composites to obtain symmetry judgments but did not rate them for attractiveness]. Figure 1 in the main article illustrates abnormalities in both face shape outline (size, width and width-to-height ratio, 4th row) and face-feature size (3rd and 4th rows) in these chimaeric faces. In another study, Swaddle and Cuthill (Ref. f) combined original full facial images and their mirror images to construct symmetrical faces, whose attractiveness was compared with the asymmetric original faces. This procedure can generate high numbers of skin blemishes in symmetrical faces (e.g. a face with a dark spot on one cheek combined with its mirror image yields paler spots on both cheeks) (Ref. g). Moreover, this study did not control facial expression and raters saw only internal features of the face, not certain secondary sexual features (jaw, chin) that are potentially important in symmetry assessment (Ref. h)

In other studies, naturally varying asymmetry measured on digitized faces has been correlated with attractiveness judgments. In two studies, symmetry predicted attractiveness (Refs i,j) whereas others have yielded, on average, very small associations between symmetry and attractiveness (Refs d,k,l). Although symmetry appears to contribute to facial attractiveness, its relative effect could be small, an issue that needs to be explored in future research.

A final approach compares ratings of facial symmetry with independent facial attractiveness ratings (Refs h,m). Perceived symmetry and attractiveness covary, possibly because people often associate symmetry and beauty (Ref. n).

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Fig. 1. Manipulations of facial symmetry. Symmetrical faces were created by averaging more than 200 corresponding facial locations on the two sides of the face, and then remapping the original face to render it symmetrical. With this procedure, left–right asymmetries in face color or texture remain in the symmetrical image, giving it ecological validity. First row: original faces. Second row: symmetrical faces made from techniques in Perrett *et al.* (in press). Third row: chimaeric faces made by combining the left side of the original face with its mirror reflection. Fourth row: same as third row except right side of original face was used (see text for explanation). (Reproduced, with permission, from Ref. 37.)

As we have seen, some attractive features clearly connote health. These include clear eyes and smooth skin, as well as non-facial features such as average body mass index[28]. The fact that people attribute greater health to attractive individuals[19,29,30] is consistent with attractiveness being the result of design that certifies health. But, as noted above, health is a broad notion in this context. Evolutionary psychologists have attempted to address the adaptationist question of whether attractiveness reflects less-obvious indicators of phenotypic condition in three main contexts: the impact on ratings of attractiveness of (1) symmetry, (2) averageness and (3) non-average sexually dimorphic features.

Facial symmetry

Fluctuating asymmetry (FA) is a departure from symmetry in traits that are symmetrical at the population level. It is thought to result from developmental instability (the inability to perfectly express developmental design) and, therefore, reflects maladaptation[31,32]. The primary causes of FA include mutations, pathogens and toxins. The evolution of humans with their co-evolving antagonists, such as pathogens and toxins in dietary plants, together with other coevolutionary antagonisms (e.g. conflicting interests between the sexes) and spontaneous mutations, accounts for genetic variation underlying developmental stability[33,34]. Fluctuating asymmetry therefore partly reflects the phenotypic and genetic condition of individuals. In Mayan men in Belize, FA is associated with incidence of serious disease[35]. The hypothesis that attractiveness assessments are sensitive to facial symmetry has been tested in a number of studies.

One approach involves monozygotic co-twin comparisons. Mealey *et al.*[36] compared the relative symmetry and attractiveness of faces of monozygotic (identical), young adult twins. Co-twins are genetically, but not developmentally, identical. The image of the face of each individual of a twin pair was split vertically down the midline, and each hemi-face duplicated, yielding left–left and right–right mirror-image facial depictions ('chimaera'). Faces were rated by two groups of observers. One group scored the similarity of mirror-image depictions of each twin while the other group were asked to judge which twin in each pair was the more attractive, using the unaltered images. For both sexes, the twins with higher similarity scores for their chimaera (i.e. those with more symmetrical faces) than their co-twins were also rated as the more attractive.

The approach of Mealey *et al.* was correlational, an important feature as the results might be particularly ecologically valid because attractiveness ratings were made only on experimentally unaltered faces. However, because symmetry was not manipulated in the faces that were judged for attractiveness, its effects could be due to covariation with other features. Early experimental studies found that natural, unaltered faces were typically preferred over computerized symmetrical faces made from them. However, more recent studies suggest that these effects are due to the nature of the manipulation used to generate symmetrical faces (see Box 1).

Two recent experimental studies have used improved methodology. Perrett *et al.*[37] used pairs of facial images comprising an original face (Fig. 1, first row) and a more symmetrical version of the original (Fig. 1, second row). Symmetrical faces were rated as more attractive. In a second experiment, normal faces were also compared with the symmetrical faces from which they derived, but all faces contained the same facial color. With texture and color symmetry thereby held constant, symmetrical faces were once again preferred. A third experiment presented all faces in a haphazard order rather than in pairs to reduce the chances of raters' awareness that symmetry was being manipulated. Again, the result that symmetrical faces were preferred was replicated.

Because faces are not actually perfectly symmetrical, raters in these studies could have preferred symmetry as a result of a preference for novelty rather than for symmetry *per se*. To address this possibility, Rhodes *et al.*[38] created symmetrical

faces by combining mirror images and original face textures but, unlike Swaddle and Cuthill[39] (and see Box 1), removed the artifact of double blemishes by retouching the images. A question of particular interest was whether people can detect subtle differences in facial asymmetry, which then influence attractiveness ratings. Four versions of each face were created: a normal face, a perfectly symmetrical face, a high-symmetry face (made by reducing the difference between the perfectly symmetrical face and the normal face by 50%) and a low-symmetry face (made by increasing the difference by 50%). Raters assessed faces for attractiveness and for appeal as a long-term mate. The degree of symmetry affected both judgments for both sexes. Moreover, attractiveness covaried with the degree of symmetry, a finding that cannot be explained by a preference for novelty. There were no sex differences in the attractiveness-rating of symmetry, but symmetry had greater effects on men's preferences for long-term mates than on women's.

Whereas these experiments demonstrate the direct effects of symmetry on attractiveness, other research suggests that symmetry can be associated with facial attractiveness for reasons other than direct effects of symmetry *per se*. In one study, Scheib *et al.*[40] asked women to rate for attractiveness either full male faces or half-faces (the other half was not shown). Half-faces contain little symmetry information, yet half-face attractiveness covaried with measured facial symmetry just as highly as full-face attractiveness. Facial symmetry covaried with a composite of men's lower face length and cheekbone prominence (with symmetrical men possessing longer lower faces relative to total face length and greater cheekbone prominence), two features thought to be affected by male hormones (see below). These features also predicted men's attractiveness. In summary, the amount of variance in facial attractiveness accounted for by the direct effects of symmetry is not currently known, but current evidence suggests that it could be small.

Enquist and Arak[41] and Johnstone[42] offered an alternative to the 'symmetry reflects condition' account, arguing that symmetry is more readily perceived by the visual system. Thus, the preference for symmetry is not the result of special-purpose design of the preference itself, but is merely a by-product of the design of the perceptual system. Perhaps the clearest evidence against this view is that women also prefer the scent of symmetrical men[43–45]. The symmetry measured in these studies was body, not facial, symmetry; however, this is irrelevant in the present context because, if symmetry were preferred as a by-product of the visual processing system, there would be no reason to expect an olfactory preference for symmetrical males. However, preference for correlated condition cues (e.g. scent) would not be surprising if symmetry were a cue for condition.

Facial averageness

Symons[13] hypothesized that facial averageness is attractive because averageness is associated with above-average performance in tasks such as chewing and breathing. In other words, natural selection has a stabilizing effect on facial features (i.e. favors the mean) and, therefore, averageness is associated with good phenotypic condition. Thornhill and Gangestad[2] suggested that preference for average trait values in some facial features (not the secondary sex traits) could have evolved because, on continuously distributed, heritable traits the average denotes genetic heterozygosity. Heterozygosity could signal an outbred mate or provide genetic diversity in defense against parasites. In fact, studies indicate that average faces are attractive but can be improved upon by specific non-average features (Box 2).

The handicap principle

The perpetual 'beauty contests' of human evolutionary history would be expected to have selected signal-receiving adaptations as well as adaptations in the outgoing signals. Evolutionary psychology addresses both the immediate workings of psychological adaptations responsible for physical attractiveness judgments, as well as adaptations that function to create, during development, the physical features that are judged.

The most prominent evolutionary theory of social signals, including sexual signals, is the handicap principle proposed by Amotz Zahavi in 1975 (Ref. 46). It explains the evolution of extravagant, and thus costly, display traits as honest signals of the ability to deal with environmental problems throughout evolutionary history. A handicap is honest in the sense that only high-quality individuals can afford it. It 'costs' high-quality peacocks less to produce and carry around an extra inch of tail than it 'costs' low-quality peacocks. Coevolution of the signaling trait and signal reception results in a situation in which it pays high-quality, but not low-quality, individuals to develop fully the costly trait (paid for by the preferences of others, e.g. mate preferences[47]). Handicap traits usually signal both the phenotypic and genotypic quality of the bearer: condition almost always shows genetic variation among individuals (i.e. is heritable) and handicaps necessarily capture the genetic variance in condition[48].

Although some traits impose purely physiological costs (e.g. the energy costs of growing an extravagant peacock tail), some handicap traits have socially mediated costs. For example, a male who throws himself into the fray of competition against other males can suffer fitness costs for doing so. Those males who are in best condition and who, therefore, are best equipped to win intrasexual competitions, suffer fewer costs, which renders willingness to engage in such competitions an honest signal of condition. In the Harris sparrow, males who possess a larger chest badge enjoy a mating advantage. A large badge itself might not be particularly costly to produce, except for the fact that males who possess one are the targets of other males' aggression; in a sense, a large badge expresses a 'willingness' to engage in intrasexual competitions. Hence, a large badge pays only for males who are intrasexually competitive, as it honestly signals condition[49].

Male facial sex-hormone markers

In many species, including humans, testosterone production and metabolism mobilizes resources for the efforts of males to attract and compete for mates[49,50]. It results in increased musculature and energy utilization through muscular activity[51] and, accordingly, draws resources away from other activities, such as immune function[52]. In men, testosterone levels increase after competitive success, suggesting that its production is sensitive to cues about ability to compete with other males[53]. Testosterone metabolism might be less costly for males who are better able to win intrasexual competitions and, therefore, testosterone and its phenotypic effects could be honest signals of condition.

Testosterone affects a number of male facial features. In pubertal males, facilitated by a high testosterone-to-estrogen

Box 2. Facial averageness: empirical studies

Initial evidence that averageness predicts attractiveness was provided by Langlois, Roggman and Musselman (Refs a,b), who found that average faces in each sex, created by compositing digitized faces, are more attractive than the majority of the individual faces from which composites were made. Critics pointed to possible confounds of averageness in these composites with facial symmetry and smoothness of skin (Ref. c). Rhodes and Tremewan (Ref. d) used a computerized caricature generator to vary overall facial averageness independent of other features caused by compositing a face, and also found average faces to be attractive. Caricaturing can exaggerate facial asymmetries, however, and thus Rhodes and Tremewan's result could be due to asymmetry covarying with non-averageness. Rhodes *et al.* (Ref. e) eliminated the potential confound by independently manipulating averageness and symmetry and found effects for both; averageness affects attractiveness even in perfectly symmetrical faces. Grammer and Thornhill (Ref. f) and Jones (Ref. g) found that measured facial averageness covaries with attractiveness. The strongest effects in Jones's cross-cultural study came from the Ache, a hunter-gatherer group.

Penton-Voak *et al.* (Ref. h) noted that self-similarity is confounded with averageness because the facial average is more similar to a person's own face than is a randomly chosen face. Participants manipulated an opposite-sex facial image along a continuum from a self-similar image (computer generated opposite sex 'sibling'), through an average face shape, to a face with opposite facial traits. No preference for self-similar or opposite faces was found.

Although average faces are attractive, many attractive features are non-average. In addition to the secondary sex traits that we discuss as hormone markers (see main article), large eyes and small noses are preferred in women (Refs g,i). These traits are not secondary sex traits. Large eyes might advertise health, as large clear whites-of-eyes can reflect an absence of infection. Studies yield mixed results concerning men's eye size (Refs j,k). Johnston and Oliver-Rodriguez (Ref. k) suggest that large eyes might be more attractive in women than in men because small eyes imply brow ridge growth and large eyes the arrest of that growth. Thus, while eyes *per se* are not secondary sex traits, their appearance could be affected by sex-typical sex hormones. Exactly what features contribute to the averageness effect remains unclear.

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ratio, the cheekbones, mandibles and chin grow laterally, the bones of the eyebrow ridges and central face grow forward, and the lower facial bones lengthen[4,34]. Large size of these male sexually dimorphic facial traits is hypothesized to be an honest signal of ability to engage in intrasexual confrontation[2,34], and they also contribute to men's perceived facial dominance[54]. Testosterone levels in teenage boys (13 and 15 year olds) correlate positively with ratings of dominance based purely on post-adolescence facial photographs[55]. However, any associations between adult circulating levels of testosterone itself, or its metabolites, and facial features remain unknown.

Trade-offs in facial traits

Studies examining the associations between attractiveness and masculine features yield mixed findings. Some show preference for masculine facial features[56], whereas others find preference for near-average or feminized facial features[57–59]. Given the signaling theory just presented, what could be the reason for this? Although masculine features might honestly signal male intrasexual competitive ability, they do not honestly signal all traits valued in a male mate. Women rate men with slightly feminized faces as more cooperative and honest, and as good parents[57]. Indeed, evidence suggests that these attributions are valid[60] and if all else is equal, these traits will be attractive to women[61].

The 'multiple fitness model' suggested by Cunningham *et al.*[7,59] proposes that attractiveness varies across multiple dimensions, rather than a single dimension, with each feature promising a different aspect of mate value. For example, some promise dominance, others promise willingness to invest in a relationship. The multiple fitness model captures the notion that different attractive features connote different fitness benefits, but does not specify the evolutionary and developmental processes whereby different traits honestly express different aspects of mate value. We suggest that masculine facial features provide an honest signal of phenotypic and genetic quality as a result of the imposed costs of those features, some of which are socially mediated. Men who are successful at attracting mates because they bear honest signals of good condition, however, could actually be less likely to invest time and other resources in offspring, and less likely to exhibit fidelity. Men with high symmetry (and developmental stability) do appear to invest less in romantic relationships than less symmetrical men, a difference thought to underlie the trade-off faced by women in preferring such men; the same might be true of men with masculine features[57,59,61–64]. For this reason, women might not prefer men who possess honest signals of good condition under all mating conditions, but only under those conditions in which the benefits of choosing such men outweigh the

costs of that choice. Thus, a feminized lower face on a man might honestly signal an individual who is willing to invest time and other resources in a relationship, and who will show fidelity, because the bearer has limited opportunity to attract multiple mates or a woman with high-mate value. Such a man might be preferred by some women under many conditions, as illustrated in the next section.

Preference changes during the menstrual cycle

Women's preferences shift during the menstrual cycle. The first such shift to be demonstrated involves the olfactory preference that women have for the scent of symmetrical men (mentioned above). This preference is specific to normally ovulating women (those not using the contraceptive pill) during the high-fertility phase of their menstrual cycle (the mid-to-late follicular phase). Women do not exhibit this preference during the low-fertility, luteal phase or when using a contraceptive pill[43–45]. This pattern makes sense if the costs and benefits of sexual encounters with men of different characteristics also vary during the cycle. Women might possess a psychological adaptation for pursuing mates with good genes for their offspring (including by 'extra-pair' sex – that outside their usual pair bond), particularly during the fertile phase of their cycle. However, as extra-pair sex can be costly and there is no opportunity for obtaining genetic benefits outside the fertile phase, this preference would not pay during the luteal phase.

Subsequent research showed a similar pattern of shift in the preference for facial features. Penton-Voak *et al.* used computer graphics to manipulate the masculinity or femininity of a composite male face by exaggerating or reducing the shape differences between male and female average faces, thereby manipulating the sexually dimorphic features affected by testosterone and estrogen[58]. In one experiment in this study, normally ovulating Japanese women preferred more feminized faces of both Caucasian and Japanese men in the low-conception phases of their cycles[58]. By contrast, women in the fertile phase preferred more masculine (in actuality, near-average) faces. Women using the contraceptive pill did not show this preference shift. In a second experiment, UK women selected their most attractive male face for short-term and long-term relationships. For a short-term mate, women showed a preference shift towards greater masculinization during the high-fertility phase. For a long-term mate, women did not show this shift. Again, these results make sense if masculinization is an honest signal of condition, albeit a sign of less willingness to invest. Thus, selection could have designed preferences to shift when the relative costs and benefits of mating with a male of best condition varied, particularly in short-term, extra-pair relationships.

In a related electrophysiological study, Oliver-Rodriguez *et al.*[65] found that the size of the P300 response of the evoked potential (a positive potential around 300 ms following presentation of a stimulus, which covaries with the emotional salience of the stimulus) of women in the fertile phase of their cycle correlated with their rating of male facial attractiveness, but not their ratings of female beauty. During the infertile phase, women's responses were undifferentiated and covaried with both male and female attractiveness. This therefore provides additional evidence that women's responses to male faces change during the menstrual cycle.

These results suggest that symmetry and honest signals of quality associated with androgens could tap common traits. As noted, provisional evidence suggests an association between symmetry and certain male facial hormone markers[40]; however, more evidence is needed. The nature of the chemical signal in male sweat in relation to developmental stability is not yet understood. One possibility is that it is related to individual variation in testosterone metabolism. Women's reactions to androgens in male sweat change during the menstrual cycle, with more favorable reactions near mid-cycle[66].

Individual differences in women's preferences

The view that cues suggest multiple valued traits, which might be differentially valued in varying circumstances, could yield predictions about how other factors affect attractiveness judgments. For example, women vary in motivation for short-term mating relationships. These individual differences probably reflect a conditional mating strategy, with women pursuing alternate mating tactics (i.e. short-term mating or long-term mating) depending on cues, because those cues, such as the amount of resources possessed by men[67], or the absence of the father during upbringing[68], predicted the tactics' effectiveness in evolutionary history. Women pursuing short-term mates value physical attractiveness more than those pursuing long-term mates[64,69,70]. Future research could address the hypothesis that women disposed to engage in short-term relationships particularly prefer honest facial signals of health and condition, whereas women disposed to engage in long-term relationships only have a particular preference for facial features associated with willingness to invest.

Other predictions are also possible. It might be that women who differ in their need for protection from men, who, by sexual coercion, might circumvent the women's mate preferences[71], also differ in their standards of attractiveness as a result of adaptation that adjusts these standards. The same may be true for women who differ in mate value to men (owing to a differential in age or attractiveness, for example)[72].

Female facial sex-hormone markers

Estrogen could be a handicapping sex hormone for women in a similar way that testosterone acts for men[30]. Estrogen signals the readiness of a woman to exert reproductive effort and is therefore a signal of fertility. Because estrogen can be expected to draw resources away from other bodily functions (e.g. immune function or repair mechanisms), it could affect mortality. The signal value of estrogen as a fertility cue could therefore result in the evolution of estrogen displays and the capacity to produce it beyond its fertility value.

A high estrogen-to-testosterone ratio in pubertal females appears to cap the growth of the bony structures that are relatively large in typical male faces, just as it caps the growth of the long bones of the body. It also results in enlargement of the lips and upper cheek area by fat deposition, similar to the estrogen-mediated fat deposition in the thighs, buttocks and breasts[30]. A variety of experimental methods have consistently shown that the most attractive female faces are associated with smallness in the bony features of the lower face, a flat middle face, large lips, and width and height in the cheeks (see Box 3). These features appear to be estrogen-dependent, although more evidence on precisely how they covary with estrogen levels is needed.

Box 3. Studies of facial hormone markers

Cunningham and colleagues (Refs a,b) first showed the importance of sex-specific facial hormone markers in attractiveness judgments by measuring features in facial photos with calipers (also Ref. c). Johnston and Franklin (Ref. d) instructed American men to create their prototype of a beautiful adult female face using facial-feature options provided in computer images. The beautiful faces had extreme secondary sex traits (e.g. full lips and high cheekbones). Johnston (Ref. e) has subsequently achieved the same results with men worldwide with access to the World Wide Web. Perrett *et al.* (Ref. f) used computer techniques to exaggerate the difference between the features of a facial composite of a large sample of women and the features of a composite made from faces of the attractive subset of the same sample. In both the UK and Japan, the most attractive faces were more feminine than average (Ref. g). Using measured features, Jones (Ref. h) found similar, but somewhat mixed, results in a number of human societies, including hunter-gatherers with limited Western contact (see also Refs i,j). Female fashion models and TV actresses, but not male models, have smaller lower faces than typical, and images of 'normal' female faces are more attractive when the lower face size is reduced (Refs h,k). Keating found that women rated as attractive tend to have full lips (Ref. l).

Johnston and Oliver-Rodriguez (Ref. m) recorded event-related potentials, which reflect neural responses, of men exposed to male and female facial depictions. Highly feminized female facial features produced larger potentials than average female facial features, but male faces produced larger responses when average. Although both sexes rate feminized facial features as more attractive in women, only men showed a large P300 response (a signal of emotional value) to highly feminized faces (Ref. n). Other research using positron emission tomography (PET) showed increased regional cerebral blood flow in two left-frontal cortical areas while men assessed attractiveness of women's faces (Ref. o). Attractiveness and unattractiveness provoked responses in different regions.

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Youth is a salient aspect of facial attractiveness in both sexes, but this preference is reputedly stronger in men because the effects of age on female fertility and reproductive value mean that female mate value is more tightly linked to age[11,13,73]. For reasons not fully understood from life-history theory, the ratio of female estrogen to androgen production changes with age and female faces masculinize with age. Female hormone markers are thus also age cues and are probably preferred partly for that reason.

Men are widely thought to place greater importance on physical attractiveness cues than do women in mating and romance because of its value as an age cue[13,74,75]. The magnitude of any sex difference, however, must be evaluated in the light of variation among women in conception risk and pursuit of short-term relationships. Women's ratings of facial attractiveness of men appear to be more variable than men's ratings of women[70], perhaps because women's ratings reflect personal circumstances more than men's (menstrual-cycle point, pursuit of short- versus long-term relationships). It might also reflect variable willingness to trade off between physical attractiveness (and thus heritable benefits from mate choice) and material benefits (and willingness to provide those benefits) in mate choice.

Mate-choice copying

Females and males can choose mates independently of other same-sex individuals' mate choices, or they can copy the mate choices of these individuals. There is now solid evidence that females of certain species of birds and fish strategically copy the mate choice of conspecific females when discrimination between potential mates is based on less than reliable cues, and when other females have greater knowledge of males[76,77]. Human studies suggest that women also copy mate choices, and more so than men (perhaps because women base attractiveness ratings on fallible cues of behavioral tendencies more than men do)[78]. Future research could examine whether female copying possesses special design features; for example, is it particularly strong when differences between potential mates are small and when potential and willingness to invest (traits that are not directly observed) are favored? Is copying less potent when genetic quality might be favored (in traits for which there could be more-reliable honest signals), for example, during the high-fertility phase of the menstrual cycle and in short-term mating contexts?

Conclusions

The adaptationist examines traits for evidence of special design: specialized features that could reveal what function, if any, the trait served in evolutionary history and led to its selection. People make aesthetic judgments of others, which has an important affect on mate and friendship choice. From an adaptationist perspective, it would be odd if the psychological features responsible for these discriminations did not serve some function in humans' evolutionary past. Adaptationists have examined a number of hypotheses subsumed under the general notion that facial-attractiveness judgments serve to discriminate an individual's phenotypic condition and, broadly speaking, health status. This review has suggested that these areas of research have been fruitful. Some areas have found considerable support for particular hypotheses (e.g. that facial symmetry increases attractiveness and an average face is attractive, even if not the most attractive). Other areas have led researchers to identify interesting patterns of preferences that are more complex than was initially anticipated (e.g. that women's preference for masculine features is not unconditional

but rather shifts with women's cycle-based fertility and that, generally, slightly feminine male faces are actually preferred).

Charles Darwin's and similar hypotheses for the evolution of mate choice – that human sexual attraction is fully explained as a means of obtaining a mate that will result in offspring with a mating advantage because of their physical attractiveness alone – are difficult to sustain in light of the evidence accumulated in these areas of research. Likewise, the hypotheses that human facial preferences: (1) are incidental effects of sensory biases arising from psychological adaptation for general object perception[41,42] or another task[79], (2) arise from adaptations that function to limit mating to conspecifics (but not high-mate-value ones) and thereby prevent maladaptive matings with heterospecific hominids and other apes[80], or (3) function to secure a mate that is unambiguously of the opposite sex[81], appear unable to account for the data. Although many questions remain unresolved, the path to truthful answers could yet follow the adaptationist perspective, which views the psychological features responsible for attractiveness judgments as special-purpose adaptations designed to discriminate the mate value of individuals throughout human evolutionary history.

Outstanding questions

- EEA-focused research is needed to clarify the relationships between facial attractiveness and health. Is individual variation in facial asymmetry, facial averageness and putative hormone markers related to measures of immunocompetence and overall condition, as predicted by the hypothesis that beauty is a health certificate?
- How do measures of symmetry, averageness and hormone markers relate to one another, and how do olfactory preferences relate to visual preferences? If they tap somewhat different aspects of condition, how do these aspects differ?
- How do specific facial features covary with behavioral traits (e.g. feminine facial features with willingness to invest), adult hormone levels and/or metabolism?
- Which specific sexually dimorphic male features do women prefer differentially during the menstrual cycle? Do women's preferences change during the cycle in other ways?
- How do individual differences or life history variations affect attractiveness judgments, and can these variations be understood from an adaptationist perspective?
- What are the details of the information processes that underlie facial attractiveness judgments, including how composite facial images are constructed to track averageness[4], relative processing of different facial features (e.g. hormone markers versus other features), and additive versus non-additive combining of information to produce a global impression[48]?

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