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THE EVOLUTIONARY PSYCHOLOGY OF FACIAL BEAUTY

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■ **Abstract** What makes a face attractive and why do we have the preferences we do? Emergence of preferences early in development and cross-cultural agreement on attractiveness challenge a long-held view that our preferences reflect arbitrary standards of beauty set by cultures. Averageness, symmetry, and sexual dimorphism are good candidates for biologically based standards of beauty. A critical review and meta-analyses indicate that all three are attractive in both male and female faces and across cultures. Theorists have proposed that face preferences may be adaptations for mate choice because attractive traits signal important aspects of mate quality, such as health. Others have argued that they may simply be by-products of the way brains process information. Although often presented as alternatives, I argue that both kinds of selection pressures may have shaped our perceptions of facial beauty.

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INTRODUCTION

> . . . [O]ur inner faculties are *adapted* in advance to the features of the world in which we dwell . . . . [O]ur various ways of feeling and thinking have grown to be what they are because of their utility in shaping our *reactions* on the outer world.
>
> (James 1892/1984, p. 11)

There are few more pleasurable sights than a beautiful face. Attractive faces activate reward centers in the brain (Aharon et al. 2001, O'Doherty et al. 2003), they motivate sexual behavior and the development of same-sex alliances (Berscheid & Reis 1998, Berscheid & Walster 1974, Feingold 1990, Rhodes et al. 2005c, Thornhill & Gangestad 1999), and they elicit positive personality attributions (the "what is beautiful is good" stereotype—Dion et al. 1972, Eagly et al. 1991, Langlois et al. 2000) and positive treatment in a variety of settings (Hosoda et al. 2003, Langlois et al. 2000). It is not surprising, therefore, that philosophers, scientists, and ordinary people have long puzzled over what makes a face attractive and why we have the preferences we do (Etcoff 1999).

A long-held view in the social sciences is that standards of beauty are arbitrary cultural conventions (Berry 2000, Etcoff 1999). Even Darwin favored this view after observing large cultural differences in beautification practices (Darwin 1998/1874). However, two observations suggest that some preferences may be part of our biological, rather than our cultural, heritage. First, people in different cultures generally agree on which faces are attractive (Cunningham et al. 1995; Langlois et al. 2000; Perrett et al. 1994, 1998; Rhodes et al. 2001b, 2002; but see Jones & Hill 1993 for weaker agreement). Second, preferences emerge early in development, before cultural standards of beauty are likely to be assimilated (Geldart et al. 1999; Langlois et al. 1987, 1991; Rubenstein et al. 1999, 2002; Samuels et al. 1994; Samuels & Ewy 1985; Slater et al. 1998, 2000).

Because preferences affect mate choice (e.g., Rhodes et al. 2005c), they may have evolved through sexual selection, whereby traits (including preferences) enhance reproductive success. Three candidates have been proposed for sexually selected preferences. The first is a preference for averageness, i.e., proximity to a spatially average face for a population. The second is a preference for bilateral symmetry. The third is a preference for sexual dimorphism, i.e., for feminine traits in female faces and masculine traits in male faces.

These traits have been proposed to signal mate quality so that preferences for them may be adaptations for finding good mates (Gangestad & Thornhill 1997; Penton-Voak & Perrett 2000a; Rhodes & Zebrowitz 2002; Thornhill & Gangestad 1993, 1999; Symons 1979). However, it is also possible that these preferences are by-products of the way brains process information, with no link between preferred traits and mate quality (e.g., Enquist & Arak 1994, Jansson et al. 2002, Johnstone 1994).

The first aim of this review is to assess the appeal of the three candidates for biologically based preferences: for averageness, symmetry, and sexual dimorphism.

The second aim is to understand what evolutionary mechanisms may have shaped these preferences and to try to resolve the debate about whether or not attractive traits signal mate quality.

WHAT MAKES A FACE ATTRACTIVE?

In his excellent book on beauty, Armstrong (2004) argues that beauty cannot be explained by a single principle, such as Hogarth's serpentine line, mathematically harmonious proportions, or a match of form to function. Similarly, there is no gold standard for facial beauty. Components of attractiveness may include averageness, symmetry, sexual dimorphism, a pleasant expression, good grooming, youthfulness (Berry 2000, Cunningham 1986, Etcoff 1999, Rhodes & Zebrowitz 2002, Thornhill & Gangestad 1999), and, for known faces, can reflect nonphysical characteristics, such as how much one likes the person (Kniffin & Wilson 2004).

There may also be different kinds of attractiveness (e.g., sexual attractiveness, attractiveness as a potential ally, cuteness) with different affective and motivational consequences (e.g., sexual arousal, competitiveness, caregiving). However, most studies have simply asked people to judge "attractiveness," which assumes some common aesthetic/affective judgment for faces of both sexes. These judgments appear to reflect sexual attractiveness for opposite-sex faces, with responses correlating almost perfectly with ratings of desirability to date (0.97) or marry (0.93) (Cunningham et al. 1990). They may also elicit judgments of sexual attractiveness (to the opposite sex) for same-sex faces, because men and women generally agree on attractiveness (Langlois et al. 2000). This agreement could reflect the assessment of sexual attractiveness in same-sex faces, to assess their danger as potential rivals for mates, or it could reflect some more generic aesthetic or affective response that is made to all faces. Agreement about which faces are attractive not only occurs between men and women, but also between people from different cultures (e.g., Langlois et al. 2000). Therefore, contrary to the popular maxim that beauty is in the eye of the beholder, preferences are not highly idiosyncratic and we can sensibly ask, what makes a face attractive?

Here I focus on averageness, symmetry, and sexual dimorphism, the three candidates for biologically based preferences. There is now a critical mass of studies, making a meta-analytic, as well as conceptual, review useful. Meta-analyses combine data across studies, giving estimates of the strength of the association (effect size) between attractiveness and given traits. They will also allow us to examine whether preferences generalize across sex and race of faces, and to assess formally the effects of potentially important methodological variables.

Separate meta-analyses were conducted for averageness, symmetry, and sexual dimorphism. The results are summarized in Table 1 (for details, see the Supplemental Material link for Electronic Appendices 1–3 in the online version of this chapter at http://www.annualreviews.org/). Effect size R's are reported, but analyses used Zr's. An initial sexual dimorphism meta-analysis showed a large effect of face sex, $F(1,38) = 26.16$, $p < 0.0001$ (0.64 ± 0.39, $N = 18$, female faces;

TABLE 1 Summary of effect size (R) statistics for the attractiveness of averageness, symmetry, and sexual dimorphism. All calculations were conducted on *Zr*'s

	Attractiveness and averageness	**Attractiveness and symmetry**	**Attractiveness and femininity**	**Attractiveness and masculinity**
All faces				
Mean effect size (ES)	0.52	0.25	0.64	−0.12
Standard deviation	0.41	0.34	0.39	0.55
95% Confidence interval	0.42–0.61	0.16–0.33	0.51–0.74	−0.35–0.14
Number of studies	20	23	10	15
Number of face samples	45	63	18	22
Mean weighted ES (by *N* faces)	0.54	0.23	0.61	0.16
Normal faces only				
Mean ES	0.40	0.23	0.64	0.35
Standard deviation	0.33	0.23	0.45	0.20
95% Confidence interval	0.29–0.51	0.17–0.30	0.41–79	0.23–0.45
Number of distinct face samples	27	42	9	10
Mean weighted ES (by *N* faces)	0.40	0.24	0.58	0.27

-0.12 ± 0.55, $N = 22$, male faces), so separate meta-analyses were conducted for female and male faces (see Supplemental Material link for Electronic Appendix 3 in the online version of this chapter at http://www.annualreviews.org/). Effects sizes are interpreted following Cohen (1977), with 0.10, 0.30, and 0.50 considered small, medium, and large, respectively.

Averageness

An average face has mathematically average trait values for a population (Figure 1). Faces that are high in averageness are low in distinctiveness. Averageness would be a good candidate for a biologically based preference, if it signals mate quality.

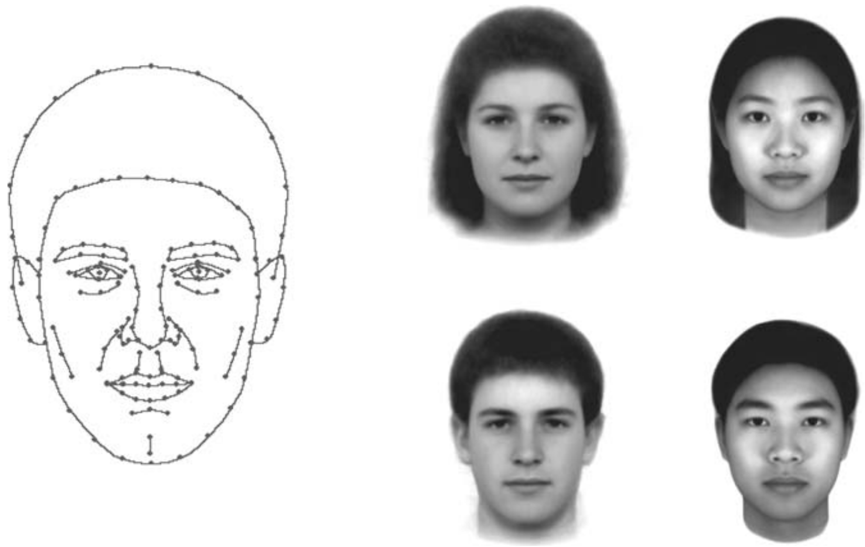

Figure 1 Landmark points used to create averaged composites. Lines have been added to illustrate how points capture the layout of internal features and the face outline, but only the points are actually used. Averaged composites of Caucasian and Chinese female (*top*) and male (*bottom*) faces. Each composite is created from 24 faces.

Several theorists have proposed that average traits reflect developmental stability, i.e., the ability to withstand stress during development (e.g., Møller & Swaddle 1997, Thornhill & Møller 1997) and heterozygosity, which may increase disease resistance (Gangestad & Buss 1993, Thornhill & Gangestad 1993). Average traits may also be functionally optimal (e.g., average nose optimal for breathing), which should improve condition (Koeslag 1990, Symons 1979). Therefore, averageness could signal aspects of mate quality, such as good condition and/or heritable resistance to disease. The proposed link between averageness and mate quality is examined below. Here I consider whether average faces are indeed attractive.

In an influential paper, Langlois and her colleagues (1990) demonstrated the appeal of computer-generated averaged composites of faces. These were generally more attractive than the component faces, and as faces were added (up to about 16), the composites became more attractive.

These counterintuitive results were met with skepticism. Surely beauty is extraordinary and cannot be explained by averageness, which is ordinary. Critics suggested that perhaps the composites were not really average (Alley & Cunningham 1991, Benson & Perrett 1992, Pittenger 1991), and they were right. The composites had nonaverage features (large eyes and lips) because feature outlines were not aligned prior to blending, and they had smooth complexions and a soft-focus look, which are attractive but not average (Benson & Perrett 1992, Little & Hancock 2002). However, composites remained attractive when features were aligned (O'Toole et al. 1999, Rhodes et al. 1999b, Rhodes & Tremewan 1996) and when same (or no) complexion appeared on all the images (Little & Hancock 2002, O'Toole et al. 1999, Rhodes et al. 1999b, Rhodes & Tremewan 1996). Therefore, the appeal of average composites is not due to enlarged features or smooth complexions.

Critics also suggested that reduction of (randomly distributed) facial asymmetries by averaging might explain the appeal of composites (Alley & Cunningham 1991). However, averageness remains attractive when the effects of symmetry are statistically controlled (Rhodes et al. 1999b) and when profiles are used, so that symmetry is unaffected (Valentine et al. 2004). Nor is the appeal of averaged composites due to their youthful appearance or pleasant expressions. These are attractive traits (Cunningham et al. 1995, Zebrowitz et al. 1993), but average faces remain attractive when these effects are statistically controlled (O'Toole et al. 1999, Rhodes et al. 1999b). Finally, the appeal of average faces is unlikely to be an artifact of combining idiosyncratic preferences across participants, because inter-rater agreement on attractiveness is high (Langlois et al. 2000). Therefore, although composites can have some nonaverage features, these do not fully explain their appeal.

Converging evidence for the appeal of average faces comes from studies using normal, unmanipulated faces. Typical faces, which are closer to the population average, are consistently rated as more attractive than distinctive faces (e.g., Light et al. 1981; Morris & Wickham 2001; O'Toole et al. 1994; Rhodes & Tremewan 1996; Rhodes et al. 1999b, 2005c; Vokey & Read 1992). Furthermore, the attractiveness of individual faces can be increased (or reduced) by moving their configurations toward (or away from) an average configuration for that sex (O'Toole et al. 1999, Rhodes et al. 1999b, Rhodes & Tremewan 1996).

The meta-analysis showed a large effect of averageness on attractiveness (0.52 ± 0.41, M $\pm$ SD; 95% CI = 0.42–0.61, $N = 45$) (Table 1). The effect size was larger for manipulated images ($0.67 \pm 0.43, N = 18$) than for real faces ($0.40 \pm 0.33, N = 27$), $t(43) = 3.20, p < 0.003$, consistent with the idea that some (nonaverage) features of composites may contribute to their appeal. However, the appeal of averageness was still moderate (0.40) for real faces. Examination of the funnel plot (see Supplemental Material link for Electronic Appendix 1 in the online version of this chapter at http://www.annualreviews.org/) suggested little publication bias. Funnel plots show effect size as a function of sample size. Variability is expected to decrease with increasing sample size, and effect sizes should be distributed symmetrically around the large sample mean. An asymmetric distribution indicates likely publication bias.

Although most studies use ratings of averageness, a few have attempted to measure it. Effect sizes were smaller for measurements ($0.09 \pm 0.36, N = 5$) than for ratings ($0.47 \pm 0.28, N = 22$), $t(25) = 2.76, p < 0.02$. Current measurement methods are poor, capturing only a limited part of a face's structure and nothing of its fattiness or skin quality (see Rhodes et al. 2005c for discussion), and ratings may be the more valid measure. They covary with physical manipulations of averageness (e.g., Rhodes & Tremewan 1996) and draw on a perceptual system that is highly sensitive to subtle facial variations. Whatever indices are used, they should be independent (e.g., rated by different participants) because effect sizes are inflated when they are not (0.73 ± 0.42, $N = 8$, nonindependent; 0.47 ± 0.38, $N = 37$, independent), t(43) = 2.66, $p < 0.02$. A medium effect size is obtained when independent indices are used with real faces (0.37 ± 0.33, 95% CI = 0.24–0.49, $N = 23$). This is the best estimate of the effect size.

The appeal of averageness did not differ significantly for male (0.57 ± 0.56, $N = 12$) and female (0.41 ± 0.20, $N = 15$) faces, t(25) = 1.24, $p = 0.225$. Most studies have combined male and female ratings because men and women agree on attractiveness (Langlois et al. 2000). However, effect sizes are lower for opposite-sex ratings (0.30 ± 0.33, $N = 13$) than when same-sex ratings are included (0.71 ± 0.51, $N = 2$, same-sex; 0.61 ± 0.40, $N = 28$, combined), F(2,40) = 4.99, $p < 0.02$ (opposite versus combined differ on Scheffé S, $p < 0.02$). Therefore, it may be wise to keep opposite-sex and same-sex ratings distinct in future studies.

Most studies have used Western faces and participants. However, average faces may also be attractive in non-Western cultures (to own-race raters) because there was no significant effect of face-race, t(27) = 0.03, $p = 0.98$ (0.59 ± 0.41, $N = 20$, Western; 0.59 ± 0.39, $N = 9$, non-Western). These results are consistent with a perceptual mechanism that favors average faces, although what is average will certainly vary between populations. Perceptual adaptation results suggest that mental representations of what is average (for a given sex and race) are constantly updated by experience (Rhodes et al. 2003b).

Clearly, average faces are attractive. However, there are some important caveats. These results don't mean that *all* attractive faces are average (contra Langlois & Roggman 1990) or that average faces are *optimally* attractive (see below). Nevertheless, average facial configurations are more attractive than most faces, and this preference must be explained.

Symmetry

Over the past decade, research on the attractiveness of facial symmetry has been prolific, motivated by the idea that symmetry advertises mate quality (e.g., Gangestad & Thornhill 1997, Gangestad et al. 1994, Palmer & Strobeck 1986, Parsons 1990, Polak 2003, Thornhill & Gangestad 1999, Thornhill & Møller 1997, Watson & Thornhill 1994). Fluctuating asymmetries (FAs) are nondirectional (random) deviations from perfect symmetry in bilaterally paired traits. In nonhuman animals, FA in body traits reflects developmental instability (inability to withstand stress during development), increasing with inbreeding, homozygosity, parasite load, poor nutrition, and pollution (Møller & Swaddle 1997, Parsons 1990, Polak 2003). In humans, body FA increases with inbreeding, premature birth, psychosis, and mental retardation (Livshits & Kobylianski 1991). If similar relationships exist for facial FA, then it could signal mate quality.

Symmetric bodies are attractive to many animals, including humans (Brooks & Pomiankowski 1994, Concar 1995, Gangestad & Simpson 2000, Thornhill &

Gangestad 1994, Watson & Thornhill 1994). But are symmetric faces attractive? Early studies suggested that they were not, with normal (slightly asymmetric) faces preferred to perfectly symmetric versions (Kowner 1996, Langlois et al. 1994, Samuels et al. 1994, Swaddle & Cuthill 1995). However, more recent studies found that perfectly symmetric faces were more attractive than the original, slightly asymmetric, faces (e.g., Perrett et al. 1999; Rhodes et al. 1998, 1999a,b) and that their appeal could not be explained by any associated increase in averageness (Rhodes et al. 1999b) or change in skin texture (Perrett et al. 1999, Rhodes et al. 1999a).

The discrepancy seems to reflect differences in how the perfectly symmetric faces were made (Rhodes et al. 1999b). In the early studies, symmetric faces were made by reflecting each hemiface about the vertical midline to create two symmetric chimeras (Kowner 1996, Samuels et al. 1994). However, these chimeras typically display structural abnormalities in aspect ratios and the sizes of midline features. For example, if the nose bends sideways, then the nose will be abnormally wide in one chimera and abnormally narrow in the other. Slight deviations from front-on views in the original photographs result in abnormally wide or narrow chimeras and abnormal eye spacing. Attractiveness decreases with deviations from average facial configurations, so these abnormalities will offset any preference for symmetry per se. When perfectly symmetric faces are made by blending normal and mirror-reversed images (Figure 2), they are more attractive than the original, slightly asymmetric faces (e.g., Perrett et al. 1999; Rhodes et al. 1998, 1999a,b). The only exception is a study by Swaddle & Cuthill (1995), but failure to control expression and remove blemishes before morphing could have contributed to failure to find a symmetry preference in this study. The meta-analysis confirmed that symmetry is attractive when blends are used ($0.43 \pm 0.32, N = 16$) but not when chimeras are used ($-0.62 \pm 0.30, N = 3$), $t(17) = 5.71, p < 0.0001$.

Converging evidence for the appeal of facial symmetry comes from studies with normal faces. Natural variations in symmetry covary with attractiveness (Jones & Hill 1993, for some ethnic groups; Grammer & Thornhill 1994; Mealey et al. 1999; Rikowski & Grammer 1999; Rhodes et al. 1998, 1999a,b; Scheib et al. 1999; Zebrowitz et al. 1996). Symmetry remains attractive when the effects of averageness are statistically controlled, which suggests that the two contribute independently to attractiveness (Rhodes et al. 1999b). The meta-analysis showed a medium effect size for normal faces ($0.23 \pm 0.23, N = 42$). All but one of these studies used independent indices of symmetry and attractiveness. The funnel plot showed no evidence of publication bias for normal faces, but a possible bias (to publish large effects) for blends (see Supplemental Material link for Electronic Appendix 2 in the online version of this chapter at http://www.annualreviews.org/).

The meta-analysis revealed no significant effects of sex of face, $F(2,60) = 1.79$, $p = 0.18$ ($0.17 \pm 0.36, N = 26$, female; $0.26 \pm 0.20, N = 27$, male; 0.40 ± 0.50, $N = 10$, combined); sex of rater, $F(2,57) = 0.40, p = 0.67$ ($0.31 \pm 0.20, N = 28$, opposite-sex; $0.13 \pm 0.01, N = 2$, same-sex; $0.28 \pm 0.35, N = 30$, combined); or race of face, $F(2,34) = 2.28$, $p = 0.12$ (0.32 ± 0.25, $N = 20$, Western;

Figure 2 Original face (*left*) and symmetric blend (*right*).

0.11 ± 0.34, $N = 9$, non-Western; 0.26 ± 0.19, $N = 8$, both). In all cases, the effect sizes were small to medium.

Although motivated by the idea that symmetry might signal mate quality, few studies have isolated FA, which is the theoretically relevant construct. This is important because directional asymmetries (DAs), which are consistent across a population and do not signal mate quality, also occur in faces (Simmons et al. 2004). Jones & Hill (1993) attempted to measure FA but measured only six traits. They also failed to demonstrate repeatability, which is important because FA is distributed as measurement error and needs to be distinguished from it (Simmons et al. 2004). Other studies claim to measure FA, but do not. For example, asymmetry is often measured by summing the offsets (from a vertical midline) of the midpoints of a few bilaterally paired landmarks (see, e.g., Grammer & Thornhill 1994). In a perfectly symmetric face, the sum would be zero. Although referred to as facial FA, this measure includes DA. Interestingly, symmetry ratings seem to reflect FA, but not DA, and may be a valid proxy for FA (Simmons et al. 2004). People apparently adapt to DA, which is consistent across a population, and notice deviations from it. Ratings change systematically when facial symmetry is manipulated, confirming their validity (see, e.g., Rhodes et al. 1999b), and are probably sensitive to more subtle facial asymmetries than are current measurement methods. Therefore, on theoretical grounds, ratings may be preferable to measurements.

The meta-analysis, however, showed no significant effect of whether symmetry was rated ($0.30 \pm 0.24, N = 14$) or measured ($0.19 \pm 0.22, N = 28$), $F(1,40) = 2.38$, $p = 0.13$.

Scheib and colleagues (1999) have argued that the apparent appeal of symmetry is not driven by perceptions of symmetry. They found an association between symmetry (of the whole face) and attractiveness when only a hemiface was shown (Scheib et al. 1999). They argued that the appeal of symmetry must therefore be mediated by the appeal of some other correlated trait because symmetry is not present in hemifaces. However, there certainly are cues to symmetry in hemifaces. For example, if more than half of the nose or mouth is visible then the face cannot be symmetric. Therefore, these results may not challenge the appeal of symmetry.

Sexual Dimorphism

Male and female faces diverge at puberty (Farkas 1988). In males, testosterone stimulates the growth of the jaw, cheekbones, brow ridges, center of the face (from brow to bottom of nose), and facial hair. In females, growth of these traits is inhibited by estrogen, which may also increase lip size (see Thornhill & Møller 1997 for a review). Because sexual dimorphism increases at puberty, sexually dimorphic traits signal sexual maturity and reproductive potential (Johnston & Franklin 1993; Symons 1979, 1992, 1995; Thornhill & Gangestad 1996).

Sexual dimorphism may also signal differences in mate quality between sexually mature individuals. In animals, large sexual ornaments can signal low parasite loadings (Hamilton & Zuk 1982, Møller 1990, Wedekind 1992), although they do not always do so (Getty 2000, Møller et al. 1999). They can also signal immunocompetence, possibly because testosterone stresses the immune system, so that only healthy males can afford large male traits (Folstad & Karter 1992, Møller et al. 1999, Peters 2000). Perhaps masculine facial traits could also signal health and immunocompetence (Thornhill & Gangestad 1993, 1999). So too could feminine traits, if high levels of female hormones also stress the immune system (see Rhodes et al. 2003a for discussion). Masculine traits may also honestly signal dominance and status, which enhance mate value (Buss 1989, Mueller & Mazur 1996).

For these reasons, a preference for masculinity in male faces (and perhaps also femininity in female faces) is a good candidate for a biologically based preference. Many animals, including humans, find extreme sexually dimorphic body traits attractive (Andersson 1994). But is sexual dimorphism attractive in faces?

FEMININITY Femininity is clearly attractive in female faces. Whether feminine traits are measured (Cunningham 1986, Cunningham et al. 1995, Johnston & Franklin 1993, Jones & Hill 1993, Koehler et al. 2004), rated (Bruce et al. 1994, Dunkle & Francis 1990, Koehler et al. 2004, O'Toole et al. 1998, Rhodes et al. 2003a), or manipulated (Johnston et al. 2001, Perrett et al. 1998, Rhodes et al. 2000), they are attractive. Furthermore, composites of very attractive female faces have more feminine features (a smaller chin and higher cheekbones) and are preferred to more average composites (Perrett et al. 1994). Exaggeration of feminine features further increases attractiveness (Johnston & Franklin 1993; Perrett et al. 1994, 1998; Rhodes et al. 2000; Russell 2003). Finally, when people generate beautiful female faces on a computer, they produce faces with more feminine traits (smaller chins, smaller lower face area, fuller lips) than average (Johnston & Franklin 1993).

Overall, femininity is strongly attractive (0.64 ± 0.39, 95% CI = 0.51–0.74, $N = 18$), with large effect sizes whether normal (0.64 ± 0.46, $N = 9$) or manipulated (0.64 ± 0.34, $N = 9$) images are used. Most studies combined data from male and female raters, so the effect of rater sex could not be examined. The preference generalizes across face race, at least for Caucasian, Asian, and Jamaican faces (Penton-Voak et al. 2004, Perrett et al. 1998, Rhodes et al. 2000), with no significant effect of face race, $F(2,8) = 0.87$, $p = 0.45$ (0.73 ± 0.34, $N = 6$, Western; 0.57 ± 0.39, $N = 4$, non-Western; 0.53 ± 0, $N = 1$, both). O'Toole et al. (1998) have suggested that female attractiveness may be virtually synonymous with femininity because attractiveness predicts time taken to classify the sex of a female face almost as well as its femininity.

Most studies used independent measures of attractiveness and femininity. Those that did not use independent measures yielded marginally larger effect sizes (0.82 ± 0.21, $N = 3$) than those that did (0.58 ± 0.38, $N = 15$), $F(1,16) = 4.29$, $p < 0.06$, supporting the need for independent measures, although the effect remained large when independent indices were used. Too few studies were available to assess possible publication bias in the funnel plot (see Supplemental Material link for Electronic Appendix 3 in the online version of this chapter at http://www.annualreviews.org/).

MASCULINITY The appeal of masculine traits is less clear. An early study using schematic faces indicated that masculinized male faces (thick brows, thin lips, square chins, and small eyes) were preferred to feminized ones (Keating 1985), but more recent studies using photographic sex continua generally show a preference for feminized male faces (Penton-Voak et al. 2004, Perrett et al. 1998, Rhodes et al. 2000; but see Johnston et al. 2001). The meta-analysis confirmed that masculinity is unattractive when these manipulated faces are used (-0.47 ± 0.51, $N = 12$). Perrett and colleagues (1998) suggest that this preference may reflect the perception of more positive personality traits (less dominant, warmer, more honest and cooperative, and more likely to be a good parent) in less masculine faces.

In these studies, masculinity was manipulated by varying the differences of an averaged male composite from an averaged female composite. But averaged male composites do not capture masculine traits well (for related concerns, see Johnston et al. 2001, Meyer & Quong 1999, Swaddle & Reierson 2002). Male traits like coarse skin textures and square jaws are generally lost in the averaging process, making male composites look less masculine than individual male faces (Little & Hancock 2002). Sex continua made using these composites may therefore tell us little about the optimal level of masculinity. They may also bias responses against the masculinized shapes that are inconsistent with the feminine skin textures displayed. When testosterone-related traits are manipulated in individual male faces, no preference for feminization (or masculinization) was observed (Swaddle & Reierson 2002).

Studies with normal faces present quite a different picture. Ratings of masculinity correlate positively with attractiveness, although the associations are weaker than for femininity (Cunningham et al. 1990, Gillen 1981, Koehler et al. 2004, Neave et al. 2003, O'Toole et al. 1998, Rhodes et al. 2003a, Scheib et al. 1999). Measurement studies also suggest that masculine traits, such as large chins, can be attractive in male faces (Cunningham et al. 1990, Grammer & Thornhill 1994, Penton-Voak et al. 2001, Scheib et al. 1999), although there are limitations to these studies. Few traits may be measured, and even then results may be inconsistent across traits (e.g., Cunningham et al. 1990), and sexual dimorphism of the chosen traits is rarely validated (for exceptions, see Koehler et al. 2004, Penton-Voak et al. 2001). The meta-analysis confirmed that masculinity is attractive for normal male faces ($0.35 \pm 0.20, N = 10$), but not for faces from sex continua (-0.47 ± 0.51, $N = 12$), $F(1,20) = 4.12, p < 0.0002$. There was no significant effect of whether or not independent indices were used for normal faces, $F(1,8) = 0.09, p = 0.77$ ($0.36 \pm 0.27, N = 5$, independent; $0.32 \pm 0.13, N = 5$, nonindependent). The funnel plot indicated a possible publication bias against small effects for normal faces (see Supplemental Material link for Electronic Appendix 3 in the online version of this chapter at http://www.annualreviews.org/).

Both average and masculine traits contribute (independently) to male attractiveness (Little & Hancock 2002, O'Toole et al. 1998). There may also be curvilinear components to the relationship between masculinity and attractiveness, indicating a preference for moderate rather than extreme levels of masculinity (Cunningham et al. 1990). There are insufficient data to determine whether masculinity is attractive to both males and females, and in non-Western faces.

MENSTRUAL CYCLE EFFECTS Women's preferences shift toward relatively masculine faces during the fertile phase of the menstrual cycle (for women not on oral contraceptives) (Frost 1994, Johnston et al. 2001, Penton-Voak et al. 1999, Penton-Voak & Perrett 2000b). Women in the fertile phase find darker (more masculine) complexions more attractive in male (but not female) Caucasian faces (although lighter complexions were always optimal) (Frost 1994). More masculine images on male-female shape continua are preferred in the fertile phase of the cycle, although the preferred image varies from feminized (Penton-Voak et al. 1999) to average (Penton-Voak & Perrett 2000b) to masculinized (Johnston et al. 2001). Although these continua do not represent masculinity veridically (see above), they do capture *relative* masculinity. Rated masculinity and dominance (Perrett et al. 1998), and the size of some male traits (chin length and eyebrow thickness) (Rhodes et al. 2000), all increase with increasing "masculinization" of the images. Therefore, relatively more masculine traits are preferred when conception is likely. This cyclic shift has been interpreted as evidence for adaptive preferences that are tuned to good genes when conception is likely (especially for short-term mates or extrapair partners) (Perrett et al. 1998). This interpretation requires that masculine traits are honest signals of mate quality, an assumption that is examined below.

Summary

Averageness and symmetry are both attractive in male and female faces, with medium to large effect sizes in all cases. Sexual dimorphism is also attractive. Femininity is attractive in female faces and is preferred to averageness. Masculinity is also attractive in male faces, although the effect is smaller than for female faces, and average traits also contribute (independently) to male attractiveness. Reported preferences for feminized male faces appear to be an artifact of using sex continua that do not adequately capture sexual dimorphism. Preferences for averageness, symmetry, and femininity generalize across race of face. It remains to be seen whether the masculinity preference generalizes across race. Finally, note that if averaged composites of male faces fail to display typical levels of masculinity, as suggested above, then the conclusion that averageness is attractive in male faces must rest primarily on the data from real faces.

THE EVOLUTION OF PREFERENCES

What selection pressures might have shaped the evolution of these preferences? To the extent that preferences influence mate choice (see, e.g., Rhodes et al. 2005c), they could be sexually selected. In sexual selection, preferences evolve because they enhance reproductive success (Andersson 1994, Barrett et al. 2002). Sexual selection can also arise from competition between same-sex individuals (displays and fights), but that component is not considered here. There are several models of sexual selection, and a central distinction is whether attractive traits signal mate quality (for reviews, see Andersson 1994, Andersson & Iwasa 1996, Cronin 1991).

Preferences could evolve in the absence of any link between attractive traits and mate quality if attractive individuals have offspring who are preferred as mates (Fisher 1915). This Fisherian runaway selection can in principle drive the evolution of extreme sexual ornaments like the peacock's tail, although it cannot explain how preferences for arbitrary traits arise initially. The model requires that both preferences and attractive traits are heritable and evolve together. Nothing is known about whether face preferences or attractive facial traits are heritable.

Alternatively, attractive traits could signal mate quality so that preferences increase offspring viability (see, e.g., Hamilton & Zuk 1982, Zahavi 1975). Attractive mates would provide direct benefits, such as resources, parental care, or reduced risk of contagion, and/or indirect genetic benefits, such as heritable resistance to disease. Evidence for genetic benefits has been found in several species (see, e.g., Møller & Alatalo 1999). The success of this "good genes" model has motivated much of the work on human face preferences and fueled suggestions that face preferences are adaptations for mate choice (Etcoff 1999; Fink & Penton-Voak 2002; Grammer et al. 2003; Johnston & Franklin 1993; Symons 1979; Thornhill et al. 2003; Thornhill & Gangestad 1993, 1999; Thornhill & Møller 1997).

However, preferences can also result as "by-products" of the way brains process information (Endler & Basolo 1998, Ryan & Rand 1993). In these models, attractive traits elicit strong responses from perceptual systems. Such models may explain why preferences emerge for some traits rather than others, and they can even explain intriguing cases of preferences for traits that don't occur in conspecifics (e.g., Basolo 1990). Although initially developed to account for the evolutionary origin of preferences (e.g., Ryan & Rand 1993), they have sometimes been presented as alternatives to mate quality accounts of the origin and maintenance of preferences (e.g., Enquist et al. 2002).

In the following two sections, I consider how face preferences might have evolved. Are preferences adaptations for mate choice, with attractive traits signaling mate quality? Or are they by-products of the way brains process information? Of course, multiple selection pressures can shape preferences (see, e.g., Weary et al. 1993), and both mate quality and by-product models may be needed to understand the evolution of these preferences.

Preferences as Adaptations for Mate Choice

Adaptations are specialized mechanisms that evolved to solve a specific problem (Williams 1966). On the mate quality account, face preferences are adaptations for mate choice. In this view, the psychological mechanisms used to assess attractiveness should show evidence of design for identifying good mates (Thornhill & Gangestad 1999). For example, faces that look healthy should be perceived as attractive, and they are (Grammer & Thornhill 1994, Henderson & Anglin 2003, Jones et al. 2001, Kalick et al. 1998). However, such results could reflect a powerful attractiveness halo effect, whereby positive traits like health are indiscriminately attributed to attractive individuals. One study has attempted to rule out a halo account by showing that symmetry looks healthy when attractiveness is statistically controlled, but it's not clear how this association reflects mechanisms for assessing attractiveness (Jones et al. 2001).

Many researchers have attempted to test the mate quality hypothesis by examining whether attractive traits currently reflect mate quality. This approach has been challenged because good nutrition and modern medicine could have broken any links with health (just as modern contraception breaks links with reproductive success) (Daly & Wilson 1999; Thornhill & Gangestad 1996, 1999). Nevertheless, it is informative about the selection pressures that maintain preferences, and to the extent that the past resembles the present, it may be informative about past selection pressures.

Quality has many components—health, intelligence, fertility, parental care potential—but most research has focused on whether attractive facial traits signal health. The anatomical complexity of faces would make them susceptible to stressors during development, and our expertise as face perceivers would make us sensitive to any resulting variation (Peterson & Rhodes 2003). So it is plausible that faces might signal health and that we would be sensitive to any such signals. We saw above that attractive faces are perceived as healthy, but is this honest advertising?

ATTRACTIVENESS AND HEALTH Meta-analyses suggest a weak association of attractiveness with mental health and a moderate association with physical health (Feingold 1992, Langlois et al. 2000). However, the latter result was based on only five studies, some of which used dubious health measures (e.g., self-reported symptoms over brief periods). More recently, Hume & Montgomerie (2001) reported a moderate association of attractiveness with physical health for women but not for men, using self-reported lifetime incidence and severity of diseases.

The study with the best lifetime health data comes from Kalick and colleagues (1998). They studied a large sample for which records of the incidence and severity of infectious diseases were available from the Institute of Human Development. Furthermore, these individuals were born in the 1920s, prior to the use of antibiotics and vaccinations that may disrupt links between attractiveness and health. There was no significant relationship between attractiveness at age 17 and health (or number of offspring) either during development or later in life. However, a recent reanalysis of these data found a moderate association between attractiveness at 17 and later (adult) health for faces below the median in attractiveness (Zebrowitz & Rhodes 2004). Interestingly, attractiveness in a mate is valued more in societies with high parasitism rates and poorer health (Gangestad & Buss 1993).

Male facial attractiveness is also associated with heterozygosity in the major histocompatibility complex, which plays an important role in immune function (Roberts et al. 2005), indicating a possible link with immunocompetence. Attractiveness is moderately associated with longevity (Henderson & Anglin 2003), weakly associated with physical fitness, independent of current exercise levels (Honekopp et al. 2004), and moderately to strongly associated with indices of sperm quality (Soler et al. 2003).

Taken together, these studies suggest links between facial attractiveness and health, at least when the organism is sufficiently challenged. However, the evidence is far from strong. Several studies need replication and many are methodologically weak, with poor health measures (e.g., Shackelford & Larsen 1999) or small samples (Henderson & Anglin 2003). Of course, not all components of attractiveness are expected to signal health (e.g., pleasant expressions). Below, I consider those that are.

AVERAGENESS AND HEALTH Marked deviations from facial averageness occur in some chromosomal disorders (Hoyme 1994, Thornhill & Møller 1997). In the Institute of Human Development sample, first studied by Kalick and colleagues

(1998), facial averageness at 17 years was moderately associated with childhood health for males and weakly associated with current annual health for females (Rhodes et al. 2001c). These associations were driven by faces below median averageness (Zebrowitz & Rhodes 2004). These results indicate a link between facial averageness and health in both clinical and nonclinical samples. However, this conclusion rests on a single nonclinical sample. Clearly, replication is needed.

SYMMETRY AND HEALTH There is little evidence that human facial symmetry signals health. The best evidence is that facial asymmetries are associated with some chromosomal disorders (Hoyme 1994, Thornhill & Møller 1997). However, without evidence that similar asymmetries do not occur in healthy individuals, we cannot be sure that facial asymmetry is a valid signal of ill health.

Furthermore, despite numerous attempts, no studies have found a convincing link between facial symmetry and health in nonclinical samples. Neither rated nor measured facial symmetry was associated with health at any point during development in the Institute of Human Development sample (Rhodes et al. 2001c). Weak associations have been reported between measured facial asymmetry and a few self-reported health symptoms over a brief period in a student sample, but the results failed to replicate in a second sample (Shackelford & Larsen 1997). Moreover, more than 1000 correlations were examined, raising the probability of type I statistical errors. Hume & Montgomerie (2001) found weak, nonsignificant associations between asymmetry (combined body and face) and self-reported lifetime health problems. No clear associations have been found between facial asymmetry and self-reported health symptoms or physiological fitness (Honekopp et al. 2004, Tomkinson & Olds 2000).

Could it be that a preference for facial symmetry evolved because of a past link with health that has been broken by modern medicine? Evidence for a link between symmetry and health in populations from harsher environments would support such a hypothesis. However, in the absence of such evidence, and the fact that links between health and averageness have not been broken, the broken link hypothesis is unconvincing.

Could these largely negative results reflect failure to isolate FA, which is the theoretically relevant variable? Perhaps yes, but symmetry ratings, which may be a good proxy for FA (Simmons et al. 2004), also showed little association with health (Rhodes et al. 2001c). Interestingly, meta-analyses have cast doubt on links between FA and health (condition) in nonhuman animals (Polak 2003, Tomkins & Simmons 2003).

SEXUAL DIMORPHISM AND HEALTH Many studies indicate a link between secondary sexual traits and health in male animals (e.g., Møller et al. 1999). Limited human data suggest a link between sexually dimorphic traits and health in male faces. In the Institute of Human Development sample, facial masculinity was weakly, but significantly, associated with adolescent health in males (Rhodes et al.

2003a). Again, this link was restricted to faces that were below the median in masculinity, suggesting that low levels of masculinity signal poor health (Zebrowitz & Rhodes 2004). Curiously, although femininity is more attractive than masculinity, no link was found with health for female faces (Rhodes et al. 2003a).

SUMMARY AND IMPLICATIONS Facial attractiveness and some of its components may have modest associations with health, although the evidence is far from overwhelming. The link may be strongest when stress is greatest, with unattractive deviations from averageness and symmetry associated with some chromosomal disorders and associations in nonclinical samples often limited to faces below the median in attractiveness. In nonclinical samples, links with health have been found for averageness and masculinity (male faces) but not for symmetry or femininity (female faces).

Before interpreting these results, we should consider their limitations. Health generally has not been measured well. Subjective and unvalidated self-report measures of illnesses or symptoms often are used. These are vulnerable to memory failures and biases whereby unattractive individuals, who may be unhappy because of poorer treatment (see, e.g., Langlois et al. 2000), recall more negative experiences (see, e.g., Teasdale & Russell 1983) than do more attractive individuals. Self-reports of recent symptoms are less susceptible to memory biases but provide limited information about health. Only the Institute for Human Development sample has health scores based on detailed, lifetime medical records. Overall, the number of studies is small, and relatively few unpublished data sets with no association between appearance and health could change the picture. More studies are needed that use samples for which objective, detailed health information is available. Samples from traditional societies, where modern medical interventions are limited, would also be informative if good health information was available.

Notwithstanding these caveats, the reported associations of health with attractiveness and some of its components suggest that preferences are not arbitrary, but instead may be adaptations for mate choice. In some cases, the associations were restricted to faces below the median in attractiveness, possibly reflecting stronger selection pressure to avoid low-quality mates than to make distinctions among higher-quality individuals.

Little is known about whether attractive individuals provide indirect genetic benefits, such as heritable resistance to disease, or direct benefits, such as reduced risk of contagion or better parental care, or both. The better treatment and outcomes afforded attractive individuals could contribute to any direct benefits. Any preference for genetically heterozygous individuals would presumably evolve via direct benefits because heterozygosity is not heritable. The same would be true for the preference for averageness, if its health benefits result from heterozygosity (Gangestad & Buss 1993, Thornhill & Gangestad 1993). However, some heritable benefits seem likely, given the heritability of health (Bouchard et al. 1990, Flint & Goodwin 1999, Reed & Dick 2003, Winkelman et al. 2000).

Femininity is the strongest component of female attractiveness, but it showed no association with health (although only one study has looked for this). Femininity may signal fertility rather than health per se (Johnston 2000, Johnston & Franklin 1993, Symons 1979). The reasoning is that high estrogen/androgen ratios are associated with both feminine characteristics (e.g., small jaw, full lips) and fertility. A preference for feminine faces, therefore, would target sexually mature females. Facial femininity could also signal individual differences in fertility in adult females, to the extent that femininity declines with age.

The hallmark of an adaptation is specialized design (Williams 1966). The shift to prefer more masculine male faces at the fertile phase of the menstrual cycle could be a specialization for obtaining indirect genetic benefits when conception is likely, given that masculinity signals health (Rhodes et al. 2003a). However, it remains to be seen whether the health benefits are heritable. An increased preference for healthy-looking faces in the luteal (postfertile) phase of the menstrual cycle has been interpreted as a specialization for obtaining direct benefits, such as reduced risk of contagion, after conception (Jones et al. 2004). Interestingly, no cyclic change has been found in the preference for facial symmetry (Koehler et al. 2002), which appears to be a poorer indicator of health.

Another possible specialization is a preference for mixed-race faces, which look healthier than single-race faces (Rhodes et al. 2005b). If parents from different races are more likely to have different locally adapted gene complexes than are parents from the same race, then a preference for mixed-race faces could be a specialization for obtaining heterozygous mates with enhanced disease resistance. Alternatively, a preference for mixed-race faces could be an inbreeding avoidance mechanism.

Restriction of preferences to opposite-sex faces could indicate specialized design for mate choice. However, there is no evidence for such restriction (see meta-analyses). Nor does a restriction of preference seem likely, given the similarity of male and female faces; its absence is certainly not evidence against preferences being adaptations for mate choice.

Preferences as By-Products of How Brains Process Information

By-product accounts attribute preferences to general information processing mechanisms that evolved through natural selection, in the absence of any link with mate quality. However, there does seem to be a link between attractive traits and health, so where does this leave by-product accounts? One possibility is that multiple selection pressures have shaped preferences (Weary et al. 1993). For example, attractive traits may arise as by-products of information processing systems but subsequently may evolve into honest indicators of mate quality (Garcia & Ramirez 2005). Alternatively, information-processing mechanisms may determine which of many honest indicators of mate quality come to be preferred.

A variety of information-processing mechanisms has been proposed to contribute to the evolution of preferences. Symmetry and averageness preferences have both been attributed to generalization effects in recognition (Enquist & Arak 1994, Jansson et al. 2002, Johnstone 1994). When trained to treat slightly asymmetric patterns as members of the same category, generalization produces strong responses to the symmetric category prototype or average. Preferences for extreme sexual dimorphism have been attributed to learning mechanisms that produce "peak shift," whereby extreme exemplars generate stronger responses than do the training exemplars in discrimination learning (Enquist & Arak 1994, Enquist et al. 2002, Guilford & Dawkins 1991, Weary et al. 1993).

Support for these accounts initially came from neural network simulations, in which preferences emerged from a variety of training situations in the absence of any link between the preferred traits and mate quality. These simulations may not behave like real biological recognition systems (Dawkins & Guilford 1995), but studies with animals and humans yield similar results (Ghirlanda et al. 2002, Jansson et al. 2002, Rhodes 1996). It remains an open question, however, whether the natural environment provides the kind of "training" needed to induce the face preferences that we have, although attempts have been made to address this question for animal preferences (Weary et al. 1993). Nor is it obvious that strong responses in recognition tasks are the same as preferences, which have affective and motivational components.

A preference for average (and symmetric) faces could also be a by-product of their subjective familiarity and a preference for familiar stimuli (Bornstein 1989, Halberstadt et al. 2003, Langlois & Roggman 1990, Langlois et al. 1994, Light et al. 1981, Rhodes et al. 2001a, Zajonc 1968). It is currently unclear just how familiarity and associated perceptual fluency (Reber et al. 2004) contribute to these preferences (Corneille et al. 2005, Langlois et al. 1994, Monin 2003), although the appeal of average faces does not seem to be a generalized mere exposure effect (Halberstadt et al. 2003; Rhodes et al. 2001a, 2005a).

If preferences are by-products of the way that brains process information, then they should not be restricted to potential mates but should occur widely for familiar stimuli. And they do. Average exemplars are attractive in every category examined (Halberstadt & Rhodes 2000, 2003; Halberstadt et al. 2003), and symmetry is attractive for many stimuli (Corballis & Beale 1976, Kubovy 2000). The generality of these preferences suggests that general information-processing mechanisms contribute to them. An interesting exception may be inverted faces, for which a symmetry preference is not found (Little & Jones 2003). However, this result is not inconsistent with recognition by-product accounts that require experience with a class of objects for preferences to emerge because inverted faces are rarely seen (see, e.g., Enquist et al. 2002).

The original goal of by-product accounts of preferences was to explain the ultimate (evolutionary) causes of preferences. However, they are also informative about their proximate causes, i.e., the psychological mechanisms that currently generate preferences. The studies reviewed above suggest that a variety of information-processing mechanisms contribute to our preferences. These include mechanisms that abstract category prototypes and generalize responses from exemplars to prototypes and learning mechanisms that respond strongly to extreme exemplars.

CONCLUSIONS AND FUTURE DIRECTIONS

An evolutionary perspective in psychology is not new, as the William James quote at the outset of this chapter indicates. However, the past decade has seen evolutionary psychology emerge as a distinct field within psychology (Barkow et al. 1992, Barrett et al. 2002, Pinker 1997). In this chapter, we have seen how an evolutionary perspective has shaped research on facial attractiveness. We have seen that averageness, symmetry, and sexual dimorphism are attractive in both male and female faces (contrary to recent claims that feminine male faces are attractive). We have seen some evidence that attractive traits may signal health, which is an important aspect of mate quality, although the evidence is far from compelling. And we have seen that the way our brains process information also shapes our preferences.

There are many exciting directions for future research. More studies are needed on whether facial attractiveness and its components signal health and other aspects of mate quality. Recently, male facial attractiveness has been linked to genetic heterozygosity at sites involved in immune function. Future studies should determine which components of male attractiveness (masculinity, averageness, symmetry) mediate this link, and whether female attractiveness is also linked to heterozygosity at these sites. A more direct test of a link between attractiveness and immunocompetence could also be done by challenging the immune system.

We know little about whether preferences generate heritable genetic benefits as proposed by the good genes model. We know little about the heritability of attractive facial traits and face preferences, as required by both Fisherian and good genes models. We know little about how facial attractiveness interacts with body attractiveness to determine overall attractiveness. We know that newborn infants prefer to look at faces that adults find attractive but know little about what traits they prefer. We know little about whether preferences change during development (e.g., at puberty). We know little about individual differences in face preferences, and whether they reflect different optimal strategies for individuals of differing mate value (Little et al. 2001, Penton-Voak et al. 2003) or self-similarity preferences (Buston & Emlen 2003, De Bruine 2004). We know that experience affects what we find attractive (Perrett et al. 2002, 2003; Rhodes et al. 2003b), but we know little about the temporal dynamics of these effects, including whether there are sensitive periods in which experience has stronger effects and whether sexual imprinting occurs in humans (Little & Perrett 2002). Clearly, the evolutionary psychology of facial attractiveness is just beginning!

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