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Symmetry and sexual dimorphism in human faces: interrelated preferences suggest both signal quality

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Symmetry and masculinity in human faces have been proposed to be cues to the quality of the owner. Accordingly, symmetry is generally found attractive in male and female faces, and femininity is attractive in female faces. Women's preferences for male facial masculinity vary in ways that may maximize genetic benefits to women's offspring. Here we examine same- and opposite-sex preferences for both traits (Study 1) and intercorrelations between preferences for symmetry and sexual dimorphism in faces (Study 1 and Study 2) using computer-manipulated faces. For symmetry, we found that male and female judges preferred symmetric faces more when judging faces of the opposite-sex than when judging same-sex faces. A similar pattern was seen for sexual dimorphism (i.e., women preferred more masculine male faces than men did), but women also showed stronger preferences for femininity in female faces than men reported. This suggests that women are more concerned with female femininity than are men. We also found that in women, preferences for symmetry were positively correlated with preferences for masculinity in male faces and that in men preferences for symmetry were positively correlated with preferences for femininity in female faces. These latter findings suggest that symmetry and sexual dimorphism advertise a common quality in faces or that preferences for these facial cues are dependent on a common quality in the judges. Collectively, our findings support the view that preferences for symmetry and sexual dimorphism are related to mechanisms involved in sexual selection and mate choice rather than functionless by-products of other perceptual mechanisms. *Key words:* facial attractiveness, preferences, sexual dimorphism, sexual selection, symmetry. *[Behav Ecol]*

Several researchers have proposed that symmetry and sexual dimorphism (masculine appearance in men and feminine appearance in women) in human faces may be cues to heritable fitness benefits and therefore relate to attractiveness (see e.g., Thornhill and Gangestad 1999). Symmetry has long been proposed to be associated with male and female genotypic quality (Jasienska et al. 2006). For many traits any deviation from perfect symmetry can be considered a reflection of imperfect development. It has then been suggested that only high-quality individuals can maintain symmetric development under environmental and genetic stress, and therefore, symmetry can serve as an indicator of phenotypic quality as well as genotypic quality (e.g., the ability to resist disease; for review, see Møller and Thornhill 1998). Both studies of real faces (Grammer and Thornhill 1994; Mealey et al. 1999; Scheib et al. 1999; Penton-Voak et al. 2001) and recent studies manipulating symmetry (Rhodes et al. 1998; Perrett et al. 1999; Little et al. 2001; Little and Jones 2003) provide evidence that symmetry is indeed found attractive.

Masculine facial traits (large jaws and prominent brows) in males are thought to be testosterone dependent and therefore may represent an honest immunocompetence handicap signaling quality (Folstad and Karter 1992), indeed masculine-faced men do report having lower incidence of disease (Thornhill and Gangestad 2006), and so should be found attractive by members of the opposite sex (e.g., Grammer and Thornhill 1994). There is some evidence that masculine male faces are found attractive (e.g., Cunningham et al. 1990; DeBruine et al. 2006; e.g., Grammer and Thornhill 1994); however, several studies have shown that feminine faces and faces of low dominance are also attractive (Berry and McArthur 1985; Perrett et al. 1998; Little and Hancock 2002). This suggests that male facial attractiveness judgements may depend on more than just cues to "good genes" for immunocompetence.

In females, estrogen-dependent characteristics of the female body correlate with health and reproductive fitness (Jasienska et al. 2004) and are found attractive (e.g., body shape, Singh 1993). Increasing the sexual dimorphism of female faces should therefore enhance attractiveness as estrogen also affects facial growth (Enlow 1982), and indeed, there is considerable evidence that feminine female faces and faces of women with high estrogen (Law-Smith et al. 2006) are considered attractive. Studies measuring facial features from photographs of women (Cunningham 1986; Jones and Hill 1993; Grammer and Thornhill 1994) and studies of manipulating facial composites (Perrett et al. 1998) all indicate that feminine features increase the attractiveness.

It is plausible that sexual dimorphism in both males and females is related to intrasexual selection or competition within a sex for mates. Association between sexual dimorphism and quality would indicate that masculine men and feminine women are better able to compete with others of their own sex. For example, high-quality sexually dimorphic individuals may be better able to physically fight off competitors or be able to travel further in the pursuit of mates than lower quality, less sexually dimorphic members of the same sex. Indeed, photographs of military cadets that were rated most dominant looking tended to achieve the highest rank later in their military careers (Mueller and Mazur 1997). It has been shown that

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when using 3 different morphing techniques that as masculinity increases in male faces, they are perceived as more dominant (DeBruine et al. 2006). It is possible that masculinity in male faces is related to competition between males and not just to attractiveness to females. It is worth noting that masculinity in male faces and femininity in female faces may potentially advertise different qualities, such as dominance versus fertility/cooperativeness.

One alternative to adaptive hypotheses for preference for symmetry and masculine male or feminine female facial features is that a preference for these traits reflects sensory bias in perception. This explanation for face preferences is often referred to as the perceptual bias view (e.g., Enquist and Arak 1993, 1994; Enquist and Johnstone 1997) and proposes that preferences are arbitrary and arise only because of the way in which the visual system operates. Certainly, preferences for symmetry have been observed for stimuli not related to mate choice such as everyday objects (Rensch 1963) and decorative art (Gombrich 1984). Computer-based neural networks trained to recognize asymmetric stimuli (stimuli with high fluctuating asymmetry) respond most strongly to novel symmetric stimuli, which are the average of training stimuli (Johnstone 1994). Preferences for symmetry can arise in a similar manner in bird species as well. Jansson et al. (2002) trained chickens to discriminate between rewarded and unrewarded stimuli. The stimuli were 2 asymmetric crosses that were mirror images of each other. On subsequent testing, chickens preferred a novel symmetric cross to either asymmetric cross despite the fact that it was never associated with reward, confirming that it is possible for symmetry preference to arise as a by-product of the visual system via perceptual experience.

Preferences for masculinity in male and femininity in female faces may also arise in a similar way. Enquist and Arak (1993) used computer neural networks to examine the mechanisms involved in signal recognition. They used these neural networks to model the evolution of female preferences for long-tailed conspecifics. Simulated female birds were trained to recognize different patterns that represented males. When shown new patterns, it was found that females recognized patterns that were similar to patterns that were first presented, but these females also "preferred" patterns similar to those first presented but exaggerated in size. This result was proposed to suggest that recognition systems could contain "hidden" preferences—training on discrimination between the categories of male and female may result in preferences for extremes of sexual dimorphism. Again, there is some evidence that the visual systems of real birds behave as predicted by computer modeling. Chickens trained to discriminate between human male and female faces show just such an effect—after training, chickens respond most strongly to faces with exaggerated sexual dimorphism, more so than they respond to the original rewarded average male and female stimuli (Ghirlanda et al. 2002). Of course, there is no reason to assume that an inherent preference can be solely attributed to sensory bias.

Rationale for the current study

Whereas many studies have examined the link between measures of quality and measured sexual dimorphism and symmetry, competing hypothesis from an evolutionary and perceptual bias view can also be usefully examined using perceptual tests. We examined 2 aspects of the perception of symmetry and sexual dimorphism, 1) preferences in same- and opposite-sex faces and 2) intercorrelation of preferences for symmetry and sexual dimorphism. Greater preferences for opposite-sex faces might be predicted if preferences are adaptations to mate choice, and this notion has received some support for symmetry preferences (Jones et al. 2001; Little et al. 2001; Penton-Voak et al. 2001; Simmons et al. 2004). On one hand, if sexual dimorphism is an advertisement of quality and important for mate choice, we might expect more extreme preferences for opposite-sex faces. On the other hand, if it is more involved in intrasexual competition, judges may assume that extremes of sexual dimorphism are attractive in the same sex. Finally, if sexual dimorphism and symmetry are advertisements of the same measure of quality, we would expect preferences for these traits to covary as individual differences increasing preference for one would be likely to increase preference for the other. If both traits advertise different aspects of quality, we might also expect a relationship as factors in the perceiver that cause individual differences in attention to different aspects of quality could also drive covariation.

METHODS

Study 1

Participants

Fifty-eight females (aged 18–30 years, mean = 21.4, standard deviation [SD] = 2.4) and 27 males (aged 18–30 years, mean = 21.1, SD = 2.9) participated in the study. Participants were students who responded to an e-mail link to an Internet study and were selected for reporting to be heterosexual.

Stimuli

To measure preferences for sexually dimorphic features, we used 20 pairs of composite face images (10 male pairs and 10 female pairs). Each pair comprised one masculinized and one feminized version of the same face (see Figure 1 for example images). Original images were 50 young adult Caucasian male and 50 female photographs taken under standard lighting conditions and with a neutral expression. The composite images were made by creating an average image made up of 5 randomly assigned individual facial photographs (this technique has been used to create composite images in previous studies, see, e.g., Benson and Perrett 1993; Tiddeman et al. 2001; Little and Hancock 2002). Faces were transformed on a sexual dimorphism dimension using the linear difference between a composite of all 50 adult males and a composite of all 50 young adult females (following the technique reported in Perrett et al. 1998). Transforms represented ±50% the difference between these 2 composites (100% would represent the complete transform and so starting from a female face + 100% toward male would make the face into a perceptually male shape). This meant that each face was transformed along the sexual dimorphism axis by the same amount, either increasing masculinity or increasing femininity, and that faces retained their identities and perceived sex (female faces remained female in appearance and male faces remained male in appearance). Composite images were made perfectly symmetric so that transforms did not manipulate symmetry.

To measure symmetry preferences, we used 30 stimulus pairs that have been used in previous studies (Perrett et al. 1999; Little et al. 2001; Little and Jones 2003), which were 15 male and 15 female Caucasian individuals between 20 and 30 years. Each pair was made up of one original and one symmetric image. All images were manipulated to match the position of the left and the right eyes. To generate the symmetric images, original images were warped so that the position of the features on either side of the face was symmetrical. Images maintained original textural cues and were symmetric in shape alone. See Perrett et al. (1999) for technical details. An example of an original and symmetrical face can be seen

Figure 1
Examples of feminized (left) and masculinized (right) female and male faces (participants viewed full color versions).

in Figure 2. The symmetry manipulation was independent of sexual dimorphism.

Procedure

Participants were administered a short questionnaire assessing age, sex, and sexual orientation, followed by the face tests. Order of rating of same- and opposite-sex faces was randomly determined for each participant. The 10 pairs of masculine and feminine faces and the 15 pairs of symmetric and asymmetric faces for each sex were presented together. Faces were shown as pairs with both order and side of presentation randomized. Participants were asked to choose the face from the pair that they found most attractive. Four options were given under each face to assess relative preferences (guess, slightly more, more, and strongly more), giving a score from 0 to 7 (0 = strongly prefer feminine/asymmetric and 7 = strongly prefer masculine/symmetric). Clicking on one of these 8 buttons moved participants on to the next face trial.

Results

Same- and opposite-sex preferences. One sample *t*-tests against no preference, or chance (3.5), were conducted for preference scores split by sex of judge. For females, this revealed significant preferences for femininity in female faces ($t_{57} = -7.9$, $P < 0.001$), masculinity in male faces ($t_{57} = 3.8$, $P < 0.001$), and symmetry in male faces ($t_{57} = 3.0$, $P = 0.004$). No significant preference for symmetry was found for females looking at female faces ($t_{57} = 1.4$, $P = 0.17$). For males, significant preferences for femininity in female faces ($t_{27} = -2.4$, $P = 0.024$) and symmetry in female faces ($t_{27} = 2.7$, $P = 0.013$) were found. No significant preferences for sexually dimorphic features ($t_{27} = 0.9$, $P = 0.38$) or symmetry ($t_{27} = 1.0$, $P = 0.35$) were found for males looking at male faces. The mean preference scores can be seen in Figure 3.

Figure 2
Examples of original (top) and symmetric (bottom) versions of male and female faces (participants viewed full color versions).

Repeated measure analyses of variance were carried out separately for preferences for sexually dimorphic features and symmetry, with sex of face as a within-participant variable and sex of rater as a between-participant variable. Age of raters was entered as a covariate in each of these analyses. For preferences for sexually dimorphic features, this revealed a significant interaction between sex of face and sex of rater ($F_{1,82} = 5.2$, $P = 0.025$), indicating that women both preferred more masculine male faces and more feminine female faces than male raters did. No other effects or interactions were significant (all $P > 0.15$). For symmetry preferences, there was also a significant interaction between sex of face and sex of rater ($F_{1,82} = 4.6$, $P = 0.035$), this time indicating that symmetry preferences were stronger when faces were of the opposite sex as the judge (individually, using paired sample *t*-tests, the difference between preferences for symmetry in male and female faces was not significant for men, $t_{25} = 1.5$, $P = 0.14$, or women, $t_{57} = -1.1$, $P = 0.27$). Again, no other effects or interactions were significant (all $P > 0.45$). The interactions can be seen in the mean preference scores in Figure 3.

Interrelation of preferences. Pearson product moment correlation coefficients were calculated between preferences for sexual dimorphism and symmetry. This was done separately for both male and female faces and split by sex of rater.

For females, this revealed significant positive relationships between preferences for symmetry in male faces and preferences for symmetry in female faces ($r = 0.35$, $P = 0.007$) and preferences for symmetry in female faces and masculinity preferences in male faces ($r = 0.29$, $P = 0.027$). Neither the correlation between symmetry and masculinity preferences in female faces ($r = -0.02$, $P = 0.88$) nor the correlation between symmetry and masculinity preferences in male faces ($r = 0.15$, $P = 0.27$) was significant.

For males, significant negative relationships were observed between preferences for symmetry and masculinity in female faces ($r = -0.48$, $P = 0.012$) and preferences for symmetry and masculinity in male faces ($r = -0.46$, $P = 0.015$). No

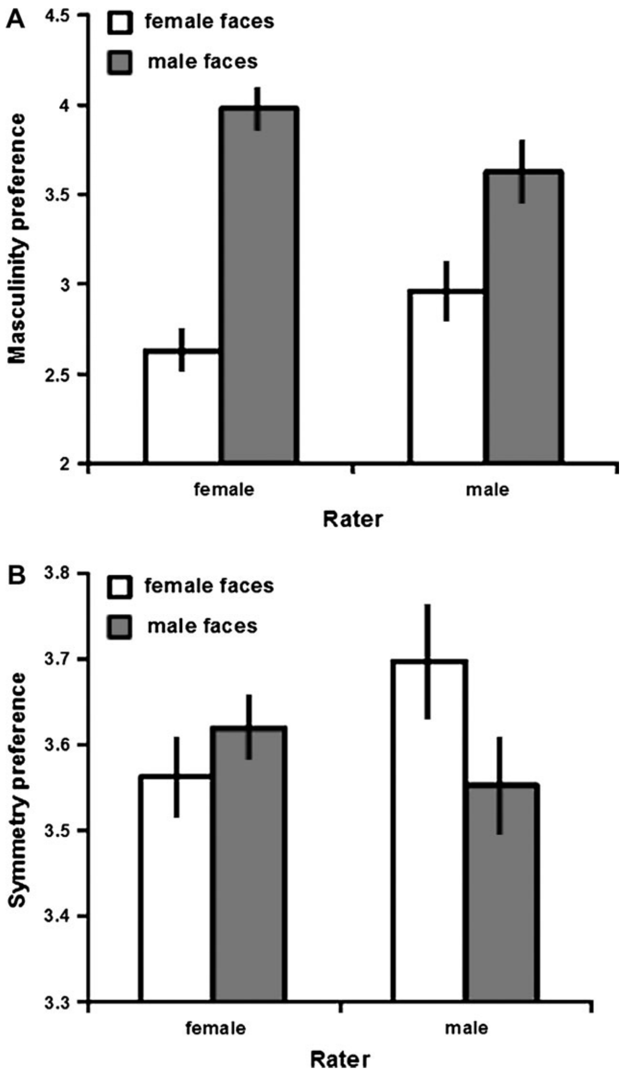

Figure 3
Preferences for masculinity (A) and symmetry (B) by sex of rater and sex of face for Study 1 (±standard error of the mean).

other correlations were significant (all $P > 0.18$). A summary of intercorrelations can be seen in Table 1.

Study 2

Participants
One hundred and seventy six females (aged 17–45 years, mean = 26.1, SD = 6.7) and 138 males (aged 17–45 years, mean = 28.3, SD = 7.6) participated in the study. Participants were volunteers, who responded to a link to an Internet study from a website and were selected for reporting to be heterosexual, >16 and <46 years of age.

Stimuli and procedure
Stimuli and procedure were identical to that of Study 1 except that participants saw only opposite-sex faces, halving the number of faces seen.

Results
General preferences. One sample *t*-tests against no preference, or chance (3.5), were conducted for preference scores. For women, this revealed significant preferences for masculinity (mean = 4.0, SD = 1.00, $t_{175} = 6.4$, $P < 0.001$) and symmetry (mean = 3.8, SD = 0.53, $t_{175} = 6.3$, $P < 0.001$) in male faces. For men, significant preferences for femininity (mean = 2.8, SD = 0.91, $t_{137} = -9.6$, $P < 0.001$) and symmetry (mean = 3.6, SD = 0.48, $t_{137} = 3.2$, $P = 0.002$) in female faces were found.

Interrelation of preferences. Pearson product moment correlation coefficients were calculated between preferences for sexually dimorphic features and symmetry. For women, this revealed a significant positive relationship between preferences for symmetry and for masculinity in male faces ($r = 0.18$, $P = 0.015$). For men, a significant negative relationship was observed between preferences for symmetry and for masculinity in female faces ($r = -0.26$, $P = 0.003$, i.e., a positive correlation between preferences for femininity and symmetry). Correlations were compared by converting *r* values using Fisher's *r*-to-*z* transform. This revealed a significant difference between these correlations ($Z = 3.90$, $P < 0.001$).

In order to examine whether these correlations were driven by regression to the mean by those expressing weak preferences for both traits due to low motivation, we examined the direction of correlations in those expressing strong preferences for symmetry or asymmetry. We computed average symmetry for both men and women (3.69) and took individuals scoring 1 average SD (0.50) above and below this mean. Rerunning the correlations revealed that the pattern of results remained the same for both men ($r = -0.651$, $N = 13$, $P = 0.016$) and women ($r = 0.343$, $N = 35$, $P = 0.044$) with symmetry preferences greater than 4.19 and men ($r = -0.628$, $N = 12$, $P = 0.029$) and women ($r = 0.438$, $N = 12$, $P = 0.155$) with symmetry preferences lower than 3.19. The *r* values for men and women remained significantly different from each other for both those with strong symmetry ($Z = 3.13$, $P = 0.002$) and asymmetry preferences ($Z = 2.56$, $P = 0.010$).

DISCUSSION

Study 1 demonstrated that both men and women have greater preferences for symmetry in opposite-sex faces than in same-sex faces. For preferences for sexually dimorphic features,

Table 1
Intercorrelations in preferences for masculinity and symmetry by sex of face for females/males

		Female		Male	
Sex of face	Rating	Masculinity	Symmetry	Masculinity	Symmetry
Female	Masculinity	—	−0.02/−0.48*	−0.07/0.13	−0.18/0.01
	Symmetry		—	0.29*/−0.18	0.35**/0.07
Male	Masculinity			—	0.15/−0.46*
	Symmetry				—

Correlation is significant (2 tailed), *0.05/**0.01.

women preferred more masculine male faces and also more feminine female faces than men did. Women did not simply have stronger preferences than men for all traits, as men had stronger preferences for symmetry in female faces than women. It was also found that preferences for symmetry and sexual dimorphism were somewhat intercorrelated. Study 2 clarified the interrelationship between preferences for sexual dimorphism and symmetry in opposite-sex faces, showing that those women who most preferred masculinity also most preferred symmetry and those males with the strongest femininity preferences also had the strongest preferences for symmetry. The correlations are not dependent on motivational differences between individuals as the pattern of correlations was identical for those expressing strong symmetry or asymmetry preferences.

The overall preferences for symmetry are in line with what has been observed in previous studies—symmetry was generally preferred in both male and female faces by male and female judges (Perrett et al. 1999; Rhodes et al. 2001). Whereas overall preferences for masculinity in male faces may conflict with previous findings showing overall preferences for femininity (Perrett et al. 1998; Penton-Voak et al. 1999; Rhodes et al. 2000; Little et al. 2001; Little and Hancock 2002), in fact variability in masculinity preferences has been highlighted in previous studies (Little et al. 2001; Little and Perrett 2002), and indeed some studies have shown preferences for masculinity using a variety of techniques (DeBruine et al. 2006).

Study 1 examined preferences in opposite-sex and same-sex faces. Preference for symmetry was more marked when women were assessing male faces than when assessing female faces and when men were assessing female faces than when assessing male faces. This suggests that symmetry is relatively more important for judgements of mate choice–relevant stimuli (i.e., opposite-sex faces) than for attractiveness judgements in general. These data are in line with previous studies. In real male faces, ratings of symmetry are more strongly associated with attractiveness for women than for men (Penton-Voak et al. 2001). For computer-manipulated symmetry, previous data have shown that female judges have greater preferences for symmetry in opposite-sex faces than in own-sex faces (Little et al. 2001). For perceptions of health, symmetry is most associated with high health for opposite-sex faces (Jones et al. 2001). The data presented here are the first to show an opposite-sex bias in attractiveness judgements for both men and women separately.

Few studies have examined same-sex preferences for sexually dimorphic features. Notably, Perrett et al. (1998) report no sex differences in male and female judgements by sex of face. Here we showed that women had stronger preferences for sexual dimorphism for both male faces, where they preferred more masculinity than men, and female faces, where they preferred more femininity than men. This may imply that women are sensitive to a competitor's femininity. Masculinity is positively related to dominance judgements in both male (Perrett et al. 1998; DeBruine et al. 2006) and female faces (Perrett et al. 1998), which is suggestive of a role in intrasexual competition. The notion of femininity being involved in intrasexual competition in females has received little attention and is an avenue for future research (Fisher 2004). It is possible that masculinity in male faces and femininity in female faces advertise different qualities, and perhaps this is related to the pattern of results. For example, if masculinity in male faces is linked to good immune function, this may lead women to prefer it more so than men, whereas if femininity in female faces has stronger links to cooperative personality traits (Perrett et al. 1998), it may again be more important for women to attend to this information. Of course, this is speculative, and the nature of what sexual dimorphism signals across male and female faces is a question for future research.

The sex difference for femininity in female faces seen in Study 1 could also reflect that men express less strong preferences for female femininity as they are less engaged in the task overall. This explanation is unsatisfying as men do express stronger preferences for symmetry in female faces than women do implying that a simple motivation difference is unlikely. The nature of the test, with limited effort required to express preference, a lack of reward for completion, and there being no right or wrong answers in preference tests detract from motivational factors explaining the sex differences seen. We also note that in Study 1, preferences for masculinity differed from chance (3.5) in opposite directions for men and women to a roughly equal degree, in fact men's preferences differed slightly more (difference from chance, men $= 0.52$, women $= 0.48$), which suggests that men are motivated to express preference at levels as strong as women.

Looking at the interrelationships between preferences for symmetry and sexual dimorphism, Study 1 presented suggestive evidence that those who preferred extremes of sexual dimorphism (more feminine for female faces and more masculine for male faces) also had stronger preferences for symmetry. In Study 1, men who preferred symmetric female faces also preferred more feminine female faces, suggesting that preferences for these traits are intercorrelated (although not significant, the correlation for female judges between symmetry and masculinity preferences in male faces was positive, $r = 0.15$).

Study 2 had a larger sample size and added clearer data on this issue. In Study 2, women who most preferred symmetry also most preferred masculinity in male faces and men who most preferred symmetry also most preferred femininity in female faces. The results then suggest that those who are attentive to one aspect of quality are also attentive to others. This may indicate that both symmetry and sexual dimorphism advertise some common aspect of quality or else that preferences for both are dependent on some common aspect of the individual judge. In terms of advertising one aspect of quality, for example, possessing genes for strong immune function may allow an individual to grow both symmetric and sexually dimorphic. Alternatively, individual differences in attention to traits signaling quality would also lead to a correlation in preferences for these traits. For example, observers who are in good condition/attractive may be more attentive to both symmetry and sexual dimorphism in faces (Little et al. 2001), driving a correlation in preferences for the traits though each trait may signal something different. Of course, a combination of these 2 factors could be in operation. Individual variation is also consistent with previous studies that have shown that there are systematic differences among women in their preferences for masculinity (Little et al. 2001, 2002) and symmetry (Little et al. 2001).

All of the current results are difficult to accommodate within a perceptual bias explanation, whereby preferences may arise from general perceptual processes (Enquist and Arak 1993; Enquist and Johnstone 1997). General mechanisms should result in equivalent preferences between men and women and between male and female faces, and sex differences in preferences are therefore problematic for such a view. Likewise, correlations between preferences are not predicted from a general processing by-product view as there is no obvious perceptual link between symmetry and sexual dimorphism. We note that here the symmetry manipulation is independent of sexual dimorphism and that images used to manipulate sexual dimorphism were all perfectly symmetrical. Explanations put forward for the bias view have argued that preferences for symmetry are derived from the fact that, on average, experience generates a symmetric template to which new faces are compared (Johnstone 1994; Jansson et al. 2002) and that preferences for masculinity in male and femininity in female faces are based on learning to discriminate male from female faces (Enquist and Arak 1993). It is possible that preferences could correlate if preferences for both were dependent on the sensitivity of the visual system and visual acuity; however, the results of Study 1, indicating that individuals prefer a single trait differently depending on the sex of face and sex of judge, suggest that this is not the case. It then appears difficult to explain why preferences for one should be related to the other from the bias view.

Our findings then appear most consistent with a mate choice–focused view of symmetry preference, which actively predicts many of the findings shown here. This view predicts that viewers should be more sensitive to symmetry when judging the attractiveness of mate choice–relevant stimuli (opposite-sex faces) than when judging the attractiveness of stimuli unrelated to mate choice (same-sex faces), as shown here. For sexual dimorphism, the data are mixed; women were more attracted to masculinity in male faces than were men but were also more attracted to femininity in female faces than were men. This is perhaps suggestive of a role of intersexual competition between women, though this remains an area for further study. The intercorrelation of symmetry and sexual dimorphism for both men and women provides further support that both may advertise some common concept of quality and provide an interesting corollary for findings showing that measured facial sexual dimorphism and symmetry are related within individuals (Gangestad and Thornhill 2003).

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REFERENCES

Benson PJ, Perrett DI. 1993. Extracting prototypical facial images from exemplars. Perception. 22:257–262.

Berry DS, McArthur LZ. 1985. Some components and consequences of a babyface. J Pers Soc Psychol. 48:312–323.

Cunningham MR. 1986. Measuring the physical in physical attractiveness: quasi-experiments on the sociobiology of female facial beauty. J Pers Soc Psychol. 50:925–935.

Cunningham MR, Barbee AP, Pike CL. 1990. What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. J Pers Soc Psychol. 59:61–72.

DeBruine LM, Jones BC, Little AC, Boothroyd LG, Perrett DI, Penton-Voak IS, Cooper PA, Penke L, Feinberg DR, Tiddeman BP. 2006. Correlated preferences for facial masculinity and ideal or actual partner's masculinity. Proc R Soc Lond B Biol Sci. 273: 1355–1360.

Enlow DM. 1982. Handbook of facial growth. Philadelphia: Saunders.

Enquist M, Arak A. 1993. Selection of exaggerated male traits by female aesthetic senses. Nature. 361:446–448.

Enquist M, Arak A. 1994. Symmetry, beauty and evolution. Nature. 372:169–172.

Enquist M, Johnstone RA. 1997. Generalization and the evolution of symmetry preferences. Proc R Soc Lond B Biol Sci. 264:1345–1348.

Fisher ML. 2004. Female intrasexual competition decreases female facial attractiveness. Proc R Soc Lond B Biol Sci. 271:S283–S285.

Folstad I, Karter AJ. 1992. Parasites, bright males and the immunocompetence handicap. Am Nat. 139:603–622.

Gangestad SW, Thornhill R. 2003. Facial masculinity and fluctuating asymmetry. Evol Hum Behav. 24:231–241.

Ghirlanda S, Jansson L, Enquist M. 2002. Chickens prefer beautiful humans. Hum Nat Interdiscipl Biosoc Pers. 13:383–389.

Gombrich EH. 1984. The sense of order: a study in the psychology of decorative art. London: Phaidon.

Grammer K, Thornhill R. 1994. Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. J Comp Psychol. 108:233–242.

Jansson L, Forkman B, Enquist M. 2002. Experimental evidence of receiver bias for symmetry. Anim Behav. 63:617–621.

Jasienska G, Lipson SF, Ellison PT, Thune I, Ziomkiewicz A. 2006. Symmetrical women have higher potential fertility. Evol Hum Behav. 27:390–400.

Jasienska G, Ziomkiewicz A, Ellison PT, Lipson SF, Thune I. 2004. Large breasts and narrow waists indicate high reproductive potential in women. Proc R Soc Lond B Biol Sci. 271:1213–1217.

Johnstone RA. 1994. Female preference for symmetrical males as a by–product of selection for mate recognition. Nature. 372:172–175.

Jones BC, Little AC, Penton-Voak IS, Tiddeman BP, Burt DM, Perrett DI. 2001. Facial symmetry and judgements of apparent health—support for a "good genes" explanation of the attractiveness-symmetry relationship. Evol Hum Behav. 22:417–429.

Jones D, Hill K. 1993. Criteria of facial attractiveness in five populations. Hum Nat. 4:271–296.

Law-Smith MJ, Perrett DI, Jones BC, Cornwell RE, Moore FR, Feinberg DR, Boothroyd LG, Durrani SJ, Stirrat MR, Whiten S, et al. 2006. Facial appearance is a cue to oestrogen levels in women. Proc R Soc Lond B Biol Sci. 273:135–140.

Little AC, Burt DM, Penton-Voak IS, Perrett DI. 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. Proc R Soc Lond B Biol Sci. 268:39–44.

Little AC, Hancock PJ. 2002. The role of masculinity and distinctiveness on the perception of attractiveness in human male faces. Br J Psychol. 93:451–464.

Little AC, Jones BC. 2003. Evidence against perceptual bias views for symmetry preferences in human faces. Proc R Soc Lond B Biol Sci. 270:1759–1763.

Little AC, Jones BC, Penton-Voak IS, Burt DM, Perrett DI. 2002. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. Proc R Soc Lond B Biol Sci. 269:1095–1100.

Little AC, Perrett DI. 2002. Putting beauty back in the eye of the beholder. Psychologist. 15:28–32.

Mealey L, Bridgestock R, Townsend G. 1999. Symmetry and perceived facial attractiveness. J Pers Soc Psychol. 76:151–158.

Møller AP, Thornhill R. 1998. Bilateral symmetry and sexual selection: a meta-analysis. Am Nat. 151:174–192.

Mueller U, Mazur A. 1997. Facial dominance in Homo sapiens as honest signalling of male quality. Behav Ecol. 8:569–579.

Penton-Voak IS, Jones BC, Little AC, Baker S, Tiddeman B, Burt DM, Perrett DI. 2001. Symmetry, sexual dimorphism in facial proportions, and male facial attractiveness. Proc R Soc Lond B Biol Sci. 268:1617–1623.

Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa R. 1999. Menstrual cycle alters face preference. Nature. 399:741–742.

Perrett DI, Burt DM, Penton-Voak IS, Lee KJ, Rowland DA, Edwards R. 1999. Symmetry and human facial attractiveness. Evol Hum Behav. 20:295–307.

Perrett DI, Lee KJ, Penton-Voak IS, Rowland DR, Yoshikawa S, Burt DM, Henzi SP, Castles DL, Akamatsu S. 1998. Effects of sexual dimorphism on facial attractiveness. Nature. 394:884–887.

Rensch B. 1963. Vesuche uber menschliche Auslosermerkmale beider Geschlecter. Z Morphol Anthropol. 53:139–164.

Rhodes G, Hickford C, Jeffery L. 2000. Sex-typicality and attractiveness: are supermale and superfemale faces super-attractive. Br J Psychol. 91:125–140.

Rhodes G, Proffitt F, Grady J, Sumich A. 1998. Facial symmetry and the perception of beauty. Psychon Bull Rev. 5:659–669.

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

Scheib JE, Gangestad SW, Thornhill R. 1999. Facial attractiveness, symmetry, and cues to good genes. Proc R Soc Lond B Biol Sci. 266:1913–1917.

Simmons LW, Rhodes G, Peters M, Koehler N. 2004. Are human preferences for facial symmetry focused on signals of developmental instability? Behav Ecol. 15:864–871.

Singh D. 1993. Adaptive significance of female physical attractiveness: role of waist-to-hip ratio. J Pers Soc Psychol. 65:293–307.

Thornhill R, Gangestad SW. 1999. Facial attractiveness. Trends Cogn Sci. 3:452–460.

Thornhill R, Gangestad SW. 2006. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. Evol Hum Behav. 27:131–144.

Tiddeman BP, Burt DM, Perrett DI. 2001. Prototyping and transforming facial texture for perception research. IEEE Comput Graph Appl. 21:42–50.