THE ROYAL SOCIETY

Facial attractiveness, symmetry and cues of good genes

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Cues of phenotypic condition should be among those used by women in their choice of mates. One marker of better phenotypic condition is thought to be symmetrical bilateral body and facial features. However, it is not clear whether women use symmetry as the primary cue in assessing the phenotypic quality of potential mates or whether symmetry is correlated with other facial markers affecting physical attractiveness. Using photographs of men's faces, for which facial symmetry had been measured, we found a relationship between women's attractiveness ratings of these faces and symmetry, but the subjects could not rate facial symmetry accurately. Moreover, the relationship between facial attractiveness and symmetry was still observed, even when symmetry cues were removed by presenting only the left or right half of faces. These results suggest that attractive features other than symmetry can be used to assess phenotypic condition. We identified one such cue, facial masculinity (cheek-bone prominence and a relatively longer lower face), which was related to both symmetry and full- and half-face attractiveness.

Keywords: developmental instability; facial masculinity; female mate choice; fluctuating asymmetry; sexual selection; male facial attractiveness

1. INTRODUCTION

Good genes sexual selection theory states that individuals will evolve preferences for mates who possess traits depicting genes that increase offspring vigour and viability. This theory has been controversial in the past (e.g. Kirkpatrick 1986), as it has been argued that natural selection effectively eliminates heritable variation in fitness such that all potential mates will possess essentially the same genes for survival (e.g. Taylor & Williams 1982; Charlesworth 1987). However, more recently, it has been found that traits associated with fitness (e.g. longevity and fecundity) tend to have much more genetic variation than ordinary morphological traits (e.g. Houle 1992; Burt 1995). Because slightly deleterious mutations occurring at a vast number of loci affect fitness, the mutation–selection balance across the genome can maintain a substantial amount of genetic variation in fitness itself (e.g. Charlesworth 1990; Charlesworth & Hughes 1999). By subjecting hosts to rapidly changing selection pressures, host–pathogen coevolution may maintain additional genetic variation in host–pathogen resistance and, hence, fitness. Recent models of good genes sexual selection suggest that the process can work (Kirkpatrick 1996). The fact that sexually selected traits tend to have an amount of genetic variation similar to fitness traits suggests that these traits have evolved as signals of overall phenotypic condition (broadly speaking, an ability to accrue and allocate energy to adaptive tasks efficiently and effectively) and have an underlying heritable component of phenotypic quality (Rowe & Houle 1996).

One marker that researchers have used to assess phenotypic condition is bilateral symmetry. The lack of symmetry in traits that are symmetrical at a population level (fluctuating asymmetry or FA) is thought to reveal an inability to resist the harmful effects of perturbations during development caused by mutations, pathogens and toxins (see the review in Møller & Swaddle 1997). Individuals with higher numbers of deleterious mutations or who are less able to resist pathogens should, on average, possess greater FA. Recent reviews of a large number of studies across a wide variety of species have indicated that FA is often associated with losses in fitness components (e.g. Leung & Forbes 1996; Møller 1997; Thornhill & Møller 1997). Moreover, in many species, males who possess greater symmetry tend to experience greater mating success (Møller & Thornhill 1998). Symmetry is partly heritable (Møller & Thornhill 1997). One estimate suggests that the underlying developmental imprecision that FA taps possesses a large amount of genetic variance, similar to that of fitness traits and sexually selected traits (Gangestad & Thornhill 1999). Together, these findings suggest that symmetry is associated with the genetic component of phenotypic condition and that mate preferences for individuals who possess good phenotypic condition result in greater mating success.

Research has shown that symmetry predicts male sexual behaviour in humans. Men with more symmetrical body measures (i.e. they have lower FA) attract more sexual partners (Thornhill & Gangestad 1994), have more partners outside their primary relationship ('extra-pair copulations' or EPCs) and were women's EPC partners more often (Gangestad & Thornhill 1997*a*) than less

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symmetrical men. Waynforth (1998) found that, in a natural fertility population of Mayans in Belize, symmetrical men tended to have more offspring and fewer serious diseases. Conversely, in a British sample, Manning *et al.* (1998) found that men with higher digit asymmetry had sperm parameters associated with lower fertility. These results suggest that, as in a variety of other species, human females respond to and prefer males who exhibit cues of good phenotypic condition and that these cues may be related to fertility.

An important question that arises from this research is whether women actually use symmetry as a cue in assessing the phenotypic condition of potential mates. Possibly, symmetry is just correlated with other markers that women use in mate choice. In some species, such as swallows (Møller 1994) and zebra finches (Swaddle & Cuthill 1994), females use cues of symmetry to choose their mates. In others, such as Japanese scorpionflies, symmetry is merely correlated with the attributes that females prefer (Thornhill 1992). Studies of body symmetry in humans (e.g. Thornhill & Gangestad 1994) have used very subtle measures of minor asymmetry (i.e. a few millimetres) in features such as ear length and elbow and foot widths. These minor asymmetries may not be detectable during normal social interaction. However, one cue that may partly 'stand-in' for symmetry is facial attractiveness. Women value facial attractiveness in their mates (Buss 1989; Scheib 1997) and Gangestad *et al.* (1994; Thornhill & Gangestad 1994) found that facial attractiveness can be predicted by the degree of symmetry in men's body traits (but see Gangestad & Thornhill (1997*a*) for one failure to replicate). These findings suggest that women use correlates of symmetry (in this case, facial attractiveness) in choosing their mates. However, symmetry itself may play a role in the assessment of attractiveness—a possibility supported by Grammer & Thornhill's (1994) finding that facial symmetry is related to the attractiveness of digitized faces (see also Rhodes *et al.* 1998; Mealey *et al.* 1999).

In the current study, we examined women's perceptions of facial attractiveness and symmetry. Women rated the attractiveness of men's faces and we tested whether these ratings were related to measures of facial symmetry. We also examined the relationship between women's attractiveness ratings and symmetry, but in faces without symmetry cues. In this case, attractiveness ratings were based only on half faces (vertical split), in which the subjects rated either the left or right half of each face. As half faces possess reduced symmetry cues, we could test whether there were cues in attractiveness that were not symmetry *per se*, but that were still related to symmetry. In addition, the subjects rated the symmetry of full faces to test whether symmetry could be detected accurately and half faces to test whether symmetry cues were still available (i.e. whether the vertical split had not completely removed the symmetry cues). Finally, we identified one possible cue in attractiveness that might be used as a marker of phenotypic condition, but that was not symmetry *per se*. This cue was an index of masculinity, as defined by two facial features, cheek-bone prominence and a longer lower face. Male cheek-bones tend to become more prominent during puberty (Enlow & Hans 1996) and a previous study has indicated that cheek-bone prominence predicts male facial attractiveness (Cunningham *et al.* 1990). Male lower face length also becomes a greater portion of the total face length during puberty, at which time a sex difference emerges (Enlow & Hans 1996). Previous research has shown that, whereas shorter lower faces are preferred in female faces, longer lower faces may be somewhat preferred in male faces (Johnston & Oliver-Rodriguez 1997). We examined whether this masculinity index was related to women's attractiveness ratings and to symmetry. The existence of both relationships would support the idea that these cues of masculinity could serve as markers of phenotypic condition.

2. METHODS

(a) *Subjects*

Seventy-nine female, University of California undergraduates completed the experiment for a course credit (mean age $= 20.51$ years and s.d. $= 2.55$ years).

(b) *Materials and procedures*

Standardized black and white pictures of undergraduate men's faces ($n = 40$) were presented in random order on a Macintosh LC. The faces were selected from a larger set using only the criteria that the face had a neutral expression and was perpendicular to the camera (i.e. without a horizontal or vertical tilt). Men, seated upright in a chair, were photographed using a 35 mm camera and a flash aimed towards the ceiling to yield relatively natural lighting conditions. The distance to the camera was constant. The men were asked to produce a neutral facial expression with their mouths closed. Symmetry and other facial measures of these men were obtained following a procedure similar to that used by Grammer & Thornhill (1994). Each man's picture was digitized (using a UC630 Umax scanner) into a Macintosh computer. Picture size was 554×554 pixels (300 K) with a resolution of 72 dpi. If necessary, scanned pictures were rotated slightly, using Adobe Photoshop software, clockwise to counterclockwise until both pupil centres were on the same y-coordinate. Each picture was slightly lightened a constant amount by Adobe Photoshop. Using Image 1.59, a measurer blind to the hypotheses placed landmark points on corresponding bilateral locations on the face: the pupils, innermost and outermost eye corners, cheek-bones (most outward projecting points on the face at or below the eyes), outer edges of the nose and mouth and jawbones (the outermost features of the face along the horizontal axis of the mouth). If the face is symmetrical in horizontal dimension, the midpoints of these lines should fall on a single vertical line. The sum of the differences between all midpoints (in pixels) was taken as a measure of horizontal facial asymmetry. Vertical asymmetry (the location of bilateral features on different horizontal planes) was measured as the sum (in pixels) of the difference in horizontal locations of each of the seven facial features. These two asymmetry measures were summed to yield a total measure of facial asymmetry. Two other facial features were measured in pixels: the lower face length (the length of the face from the pupils to the tip of the chin) as a proportion of the total face length and cheek-bone prominence, the ratio of the width of the face at the cheek-bones divided by the width of the face at the level of the mouth (Cunningham *et al.* 1990). The measurements of each of these facial features were highly reliable with correlations between measurers of at least 0.85 (Grammer & Thornhill 1994; Rikowski & Grammer 1999).

Three-stimuli sets were used: full faces, left half faces and right half faces (left or right indicates the man's side of his face). The two sets of half faces were created in Adobe Photoshop by vertically splitting each face. A line was drawn down the middle of the face, going through the key points of the middle of the nose tip and the centre of the lips (e.g. through the 'v' of the upper lip). In only one case was it not possible to line these up and this picture was eliminated from the stimulus set. Stimulus pictures were presented one at a time and the subjects were required to rate the physical attractiveness or symmetry of each face on a seven-point Likert scale that appeared below the face. A new face would appear only after the previous face had been rated. Each subject began the experiment with a practice task of rating how funny a cartoon was. Once this was rated, the experimenter left the room and the subject completed the experiment alone.

The subjects were given the task of rating either the attractiveness or symmetry of the faces. Twelve women rated the attractiveness ('how attractive is this face?') of full faces, 12 more rated left half faces and a third group of 12 rated right half faces. None of the subjects reported difficulty with this task. Fifteen women rated the symmetry ('how symmetrical is this face?') of full faces, 14 more rated left half faces and a third group of 14 rated right half faces. Not surprisingly, a few subjects reported difficulty with rating the symmetry of half faces and completed the task after being instructed to imagine what the full face would look like.

3. RESULTS

(a) *Assessment of facial attractiveness*

Attractiveness ratings were calculated by averaging across subjects within each group for each man's full face, left half face or right half face. The reliabilities were 0.92, 0.91 and 0.91, respectively. Pearson product-moment correlations were used to test for relationships between ratings of attractiveness and measures of facial symmetry. For all correlations reported, the effects of age and age squared were partialled, as men's age may affect their attractiveness.

The men's full-face attractiveness was positively related to their measured facial symmetry ($r(36)=0.48$ and $p=0.002$), an effect which replicates Grammer & Thornhill's (1994) finding with digitized faces. To examine whether removal or reduction of symmetry cues attenuated the correlation of attractiveness with symmetry, we correlated half-face attractiveness with facial symmetry. The results showed that both left and right half-face attractiveness were correlated with facial symmetry ($r(36)=0.50$ and 0.38 and $p=0.001$ and 0.020, respectively). The correlations of symmetry with left and right half-face attractiveness did not differ significantly ($t(35)=1.15$, n.s.). The mean correlation between half-face attractiveness and symmetry was 0.44, similar to the correlation between full-face attractiveness and symmetry (0.48). These findings thus suggest, first, that facial attractiveness could be used by women to assess phenotypic quality in potential mates, because facial attractiveness was related to actual measures of facial symmetry. Second, there are cues in faces that are related to symmetry and, hence, may be markers of good genes, but the cues are not symmetry *per se*; moreover, these cues affect women's attractiveness assessments.

(b) *Assessment of facial symmetry*

As with the attractiveness ratings, the symmetry ratings were averaged across subjects within each group to yield ratings for each man's full face, left half face or right half face. The reliabilities were 0.84, 0.74 and 0.77, respectively. (These lower reliability scores suggest that the symmetry ratings were harder to make than attractiveness ratings.)

The subjects' symmetry ratings of full faces were only weakly related to the actual measures of facial symmetry ($r(36)=0.26$ and $p=0.121$). No relationship was found between the subjects' ratings of right half-face symmetry and the actual measures of symmetry ($r(36)=0.06$ and $p=0.720$). The subjects' symmetry ratings of left half faces were weakly related to the actual measures of symmetry ($r(36)=0.30$ and $p=0.067$). Nonetheless, the correlations between actual symmetry and judged symmetry of the right and left half faces were not significantly different ($t(32)=1.32$, n.s.). These findings suggest that the subjects were very poor at detecting facial symmetry, even when explicitly instructed to do so. Note, however, there was a weak association observed for the left half faces, though not significantly higher than that for right half faces.

(c) *The masculinity index*

The masculinity index was calculated by standardizing the two facial measures of cheek-bone prominence and relative lower face length and summing them into a single index.

This index was positively related to women's attractiveness ratings of full faces ($r(36)=0.48$ and $p=0.002$), right half faces ($r(36)=0.34$ and $p=0.040$) and left half faces ($r(36)=0.49$ and $p=0.002$). (The correlations with the right and left half-face attractiveness did not significantly differ ($t(35)=1.42$, n.s.).) Hence, men with more masculine features tended to be rated as more attractive. Second, this masculinity index was also positively related to the actual measures of facial symmetry ($r(36)=0.35$ and $p=0.031$), indicating that women could use these features, which were available in both full and half faces, as cues of phenotypic condition.

4. DISCUSSION

Symmetry has been found to be associated with human facial attractiveness and men's sexual success. In most studies, facial symmetry was not manipulated, which leaves open the question of whether symmetry serves as a cue that women use or, instead, covaries with cues of attractiveness. The current study found evidence that symmetry covaries with the cues that people use. Facial symmetry correlated with the attractiveness of half faces, for which the cues of symmetry were essentially removed. Indeed, the mean correlation between symmetry and half-face attractiveness (0.44) was close to the correlation between symmetry and full-face attractiveness (0.48). While these results do not show that symmetry does not serve as a cue whatsoever (see Rhodes *et al.* 1998; Mealey *et al.* 1999), they suggest that symmetry is not the main cue by which individuals perceive phenotypic quality.

Another interpretation could be that other cues are used to assess attractiveness when symmetry cues are removed in the half faces. This would require that these other cues account for similar amounts of variance in attractiveness as the symmetry cues might have in the full faces.

We explored the possibility that the cues by which women judge phenotypic condition include facial features indicating sexual differentiation of the male face—a relatively longer lower face and prominent cheek-bones (Enlow & Hans 1996). We found that a composite index of these features correlated with both symmetry and attractiveness and, thus, may partly mediate the association between facial symmetry and attractiveness. Although further work is needed, these results are consistent with the notion that more masculine faces are more symmetrical. Recently, Penton-Voak *et al.* (1999) reported that relatively more masculine male faces are seen as more attractive, but only by women who are in the fertile phase of their menstrual cycle. If masculinity of the face covaries with symmetry, this finding accords with Gangestad & Thornhill's (1998) finding that women prefer the scent of symmetrical men, but only during their fertile phase (see also Thornhill & Gangestad 1999). It is possible that female assessment of male attractiveness through multiple modalities varies with their fertility such that markers of 'good genes' are particularly preferred when conception is possible (Gangestad & Thornhill 1998). One reason why more masculine features may be associated with symmetry is that they are possible markers of testosterone production and metabolism, the effects of which (e.g. muscularity) are expensive to maintain (though it should be noted this idea has yet to be tested empirically). These markers may thus serve as honest signals of ability to bear a cost (e.g. Grafen 1990; Folstad & Karter 1992). Other research has found that more symmetrical men are seen by themselves and their partners as more muscular (Gangestad & Thornhill 1997*b*) and have more physical fights with other men (Furlow *et al.* 1998; see also Simpson *et al.* 1999). Success in intrasexual competition (and predictors of that success) may affect female choice by similarly being an honest signal of ability to invest effectively in a costly activity (see Trivers 1972; Andersson 1994). It should be noted that this masculinity measure is only one of multiple facial cues that may be useful in assessing potential mates. For example, skin texture may signal information about health and underlying genotypic quality. Clearly, future research is needed to identify the facial cues used in mate choice more fully. Future research should also seek to specify the nature of the cognitive processes that combine individual facial traits into a global attractiveness judgement (see Miller & Todd 1998).

However, these findings do not address the question of why symmetry itself appears not to be the most powerful cue used by female perceivers in assessing male phenotypic condition and developmental precision. Recently, attention has been drawn to the fact that asymmetry of single traits is not highly correlated with underlying developmental imprecision. The effect of developmental error has a random component. Some individuals presumably have more error than others, but the random component of the effect of error accounts for much of the variance in a single trait (e.g. Whitlock 1996, 1998; Van Dongen 1998). Recently, Gangestad & Thornhill (1999) estimated that less than 10% of the variance in a single trait's asymmetry is due to individual differences in developmental imprecision. Aggregation over several traits' asymmetries is needed to tap a substantial amount of variance in developmental imprecision. The face itself is comprised a number of traits whose symmetry could aggregate into an overall impression of symmetry. Quite possibly, however, facial cues other than symmetry (e.g. masculinity) may actually correlate more highly with developmental imprecision than symmetry itself. Of course, even if this is so, measuring symmetry remains a useful way for researchers to assess developmental imprecision and phenotypic condition. However, they should not assume that their subjects have evolved to use symmetry as a powerful indicator.

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