

Symmetry, sexual dimorphism in facial proportions and male facial attractiveness

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Facial symmetry has been proposed as a marker of developmental stability that may be important in human mate choice. Several studies have demonstrated positive relationships between facial symmetry and attractiveness. It was recently proposed that symmetry is not a primary cue to facial attractiveness, as symmetrical faces remain attractive even when presented as half faces (with no cues to symmetry). Facial sexual dimorphisms ('masculinity') have been suggested as a possible cue that may covary with symmetry in men following data on trait size/symmetry relationships in other species. Here, we use real and computer graphic male faces in order to demonstrate that (i) symmetric faces are more attractive, but not reliably more masculine than less symmetric faces and (ii) that symmetric faces possess characteristics that are attractive independent of symmetry, but that these characteristics remain at present undefined.

Keywords: fluctuating asymmetry; facial attractiveness; facial sexual dimorphism

1. INTRODUCTION

Theories of sexual selection suggest that 'good genes' in a potential partner may be advertised through some kind of indicator mechanism. Preferences for partners with traits that reliably indicate heritable benefits in offspring should be favoured. Such 'good genes' theories have become more popular with empirical demonstrations of heritability of fitness (e.g. Petrie 1994) and theoretical models demonstrating that indicator mechanisms are possible under conditions characterized by rapidly changing selection pressures (e.g. host-parasite coevolution) (Andersson 1994; Kirkpatrick 1996).

One possible indicator that has received widespread attention is bilateral symmetry, which is thought to be an indicator of developmental stability. Fluctuating asymmetries (asymmetry in traits that are on average symmetric in a population) (Van Valen 1962) result from an organism's failure to cope with various inclement environmental (e.g. malnutrition and parasitization) and genetic (e.g. mutation) factors (Møller 1997). Better 'quality' individuals may resist environmental hazards better than poorer quality individuals and some of this quality may be heritable (Møller & Thornhill 1997). As such, a preference for symmetry in mate choice may have been favoured by selection. Males with low levels of fluctuating asymmetry have more mating success across multiple species and taxa (Møller & Thornhill 1998).

Researchers have examined symmetry with respect to human behaviour and physical attractiveness (see Gangestad & Simpson (2000) for a review). For example, men with low levels of body fluctuating asymmetry report more sexual partners and are involved in more extra-pair sexual encounters than men with greater levels of asymmetry (Gangestad & Thornhill 1994; Thornhill & Gangestad 1994). Given the central role of the face in human social life and the importance of the face in

physical attractiveness judgements of potential partners, it is unsurprising that several studies have addressed the role of facial symmetry in attractiveness. Studies of asymmetry in natural faces (e.g. Grammer & Thornhill 1994; Mealey *et al.* 1999) and digitally manipulated stimuli (e.g. Perrett *et al.* 1999; Rhodes *et al.* 1998) indicate that facial symmetry is positively correlated with attractiveness in both male and female faces.

Recently, Scheib *et al.* (1999) presented data suggesting that symmetry is not an important cue to attractiveness in male faces, although it is a correlate. Raters preferred faces that originally possessed high levels of symmetry when presented with only left or right half faces (faces split down a vertical midline bisecting the nose and mouth). As these faces had no or at most minor cues to symmetry, Scheib *et al.* (1999) concluded that a correlate of symmetry that is visible in half faces must drive attractiveness judgements. They reported that facial 'masculinity' (as quantified by an index of two measured facial proportions, i.e. cheekbone prominence and relative lower face size) correlates with both attractiveness and symmetry and is visible in half faces. Hence, masculinity seems to be a likely cue to attractiveness in male faces. Correlations between trait size and symmetry have been reported in some avian species and fit well with indicator models of sexual selection (e.g. Møller & Höglund 1991; see Balmford *et al.* (1993) for another interpretation). Masculine facial traits (large jaws and prominent brows) in males are thought to be testosterone dependent and, therefore, may represent an honest immunocompetence handicap (Folstad & Karter 1992). As immunocompetence should be linked to developmental stability, a correlation between both symmetry and masculinity is predicted.

However, the role of facial masculinity in attractiveness judgements is disputed. Cunningham *et al.* (1990) and Grammer & Thornhill (1994) used facial measurements and found a female preference for large jaws in males. Masculine features, such as a large jaw and a prominent brow ridge, are also reliably associated with ratings of

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dominance in photographic, identikit and composite stimuli by male and female raters (McArthur & Apatow 1983–1984; McArthur & Berry 1987; Berry & Brownlow 1989; Berry & Wero 1993; Perrett *et al.* 1998). Facial dominance appears to correlate with status in some human hierarchies (Mueller & Mazur 1997) and facial dominance in adolescent males is associated with an earlier age at first copulation (Mazur *et al.* 1994). Nonetheless, the relationship between facial dominance and attractiveness is unclear—some studies find a positive relationship (Keating 1985) while others find the opposite (McArthur & Apatow 1983–1984; Berry & McArthur 1985; Perrett *et al.* 1998). Other studies propose that a mixture of masculine and feminine traits are found attractive (Cunningham *et al.* 1990) or that preferences for masculinity or femininity vary across the menstrual cycle as a function of the probability of conception (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000).

The aim of the current study was to investigate the relationship between symmetry, masculinity and attractiveness in male faces further. Study 1 investigated the relationship between facial symmetry and attractiveness in a sample of male faces.

Study 2 aimed to quantify sex differences in the facial proportions visible in frontal facial photographs by measuring characteristics from a sample of male and female faces. This allowed the relationship between masculine features, symmetry and attractiveness to be studied and, secondarily, provided a composite measure of facial masculinity.

Finally, in study 3 we investigated whether the correlates of symmetry in faces can be extracted using an alternative, computer graphics technique. Composite images can be generated from samples of facial photographs using warping and blending techniques. Such composite images tend to retain properties that the sample faces have in common, e.g. sex (Perrett *et al.* 1994, 1998) or age (Burt & Perrett 1997), but lose the identities of individuals who make up the composite. This technique can be usefully applied to studies of facial symmetry, as there are no reported directional asymmetries in human faces at rest. Hence, a facial composite made from low-symmetry individuals should have a very low level of asymmetry, as should a composite constructed from individuals with high facial symmetry. Correlates of symmetry such as large jaws or other markers of masculinity should still differ between the two composite images.

If, as Scheib *et al.* (1999) suggested, these cues are important to attractiveness judgements, raters should find the 'high-symmetry' composite both more masculine and more attractive than the 'low-symmetry' composite. As these techniques generate full facial stimuli rather than half faces, the task may have somewhat more ecological validity than the test employed by Scheib *et al.* (1999).

2. METHODS

(a) Study 1

Sixty-six young (mean age 21.3 years), Caucasian, adult male undergraduates were photographed under standard conditions with diffuse flash lighting from two lateral flashguns. Images were captured on a digital camera at a resolution of 1200 × 1000 pixels. Sitters assumed a neutral expression and removed

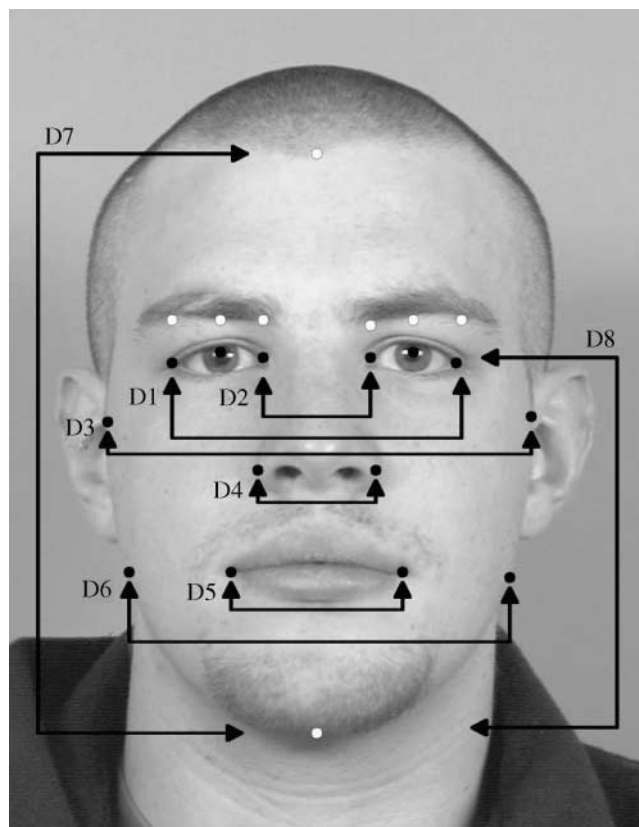


Figure 1. Points used in the calculation of facial metric measurements. Filled circles, points used in symmetry calculations; open circles, additional points used in measurements of scaled sexual dimorphism. Lines specify the dimensions used in masculinity calculations (see table 1)

occluding hair from the face as much as was possible. Each image was then normalized on the interpupillary distance. Some additional biographical information was collected (height, weight and age).

(i) Attractiveness judgements

The facial images were presented in a random order on computer and rated for attractiveness by 21 subjects (11 female) on a seven-point Likert scale (1 = very unattractive and 7 = very attractive). The subjects showed high consistency in their attractiveness judgements (Cronbach's $\alpha = 0.84$).

(ii) Symmetry assessment

Two techniques were used for assessing the symmetry of the individual male faces. A facial-metric technique estimated horizontal and vertical asymmetry from x - y coordinates of seven bilateral points using techniques described in Scheib *et al.* (1999) and elsewhere (see figure 1).

The second 'perceptual' measure of symmetry involved creating two chimaeric stimuli from each original face (Mealey *et al.* 1999). Each individual image was rotated so that the centre of the pupils lay on the same y -coordinate and then the face was split vertically along a line bisecting the distance between the pupils, thereby creating left and right half faces. These half faces were mirrored, creating double left (L-L) and double right (R-R) chimaeric images (figure 2). L-L and R-R image pairs were presented to ten subjects (five female) who rated the faces for 'similarity' on a seven-point Likert scale (1 = very dissimilar and 7 = very similar). High ratings of similarity indicate small

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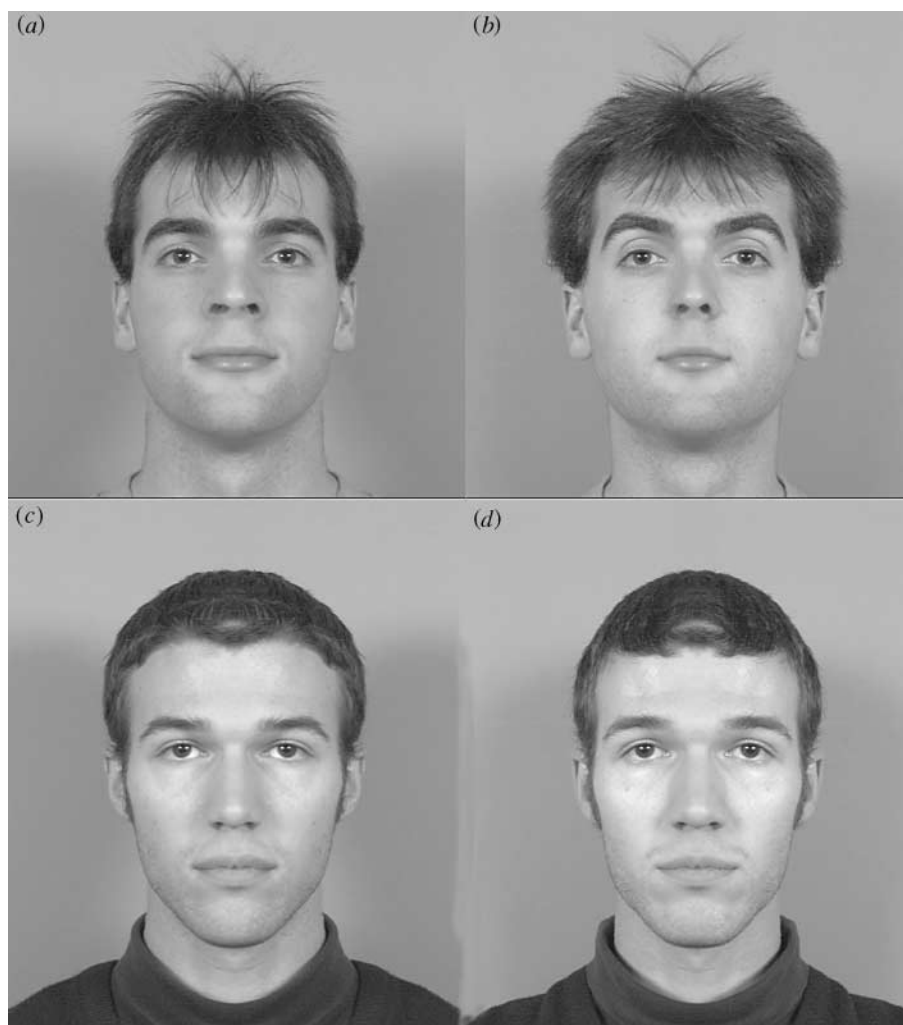


Figure 2. Double left (L–L) and double right (R–R) chimaeric stimuli from a low-symmetry face (top) and a high-symmetry face (bottom).

perceptual differences between L–L and R–R chimaeric faces, which may reflect high facial symmetry. The subjects showed very high consistency in this task (Cronbach's $\alpha=0.93$). Measured asymmetry and rated perceptual symmetry were significantly correlated (Spearman's $r_s = -0.477$, $p < 0.001$ and $n = 66$).

(b) Study 2

It has been proposed that the size of sexually dimorphic features correlates with both facial symmetry and attractiveness. In order to test this hypothesis, facial-metric measures were taken from 27 feature points marked onto facial features on the 66 male faces used in study 1 and a further 49 female faces taken under the same photographic conditions (see figure 1). The identification of these features has been found to be reliable in several earlier studies (e.g. Grammar & Thornhill 1994; Scheib *et al.* 1999). The female and male faces were standardized to the same interpupillary distance (100 pixels) in order to allow comparison between male and female facial proportions. This standardization technique prevents measurement of absolute trait size (all traits are scaled relative to the distance between the pupils), but does eliminate the possibility that small variations in head distance from the camera will lead to erroneous measurements. The measurements taken are reported in table 1.

(c) Study 3

An alternative method of assessing the face shape correlates of facial symmetry is to use digital averages (composites) of multiple individual faces. As human faces have no reported directional asymmetry at rest in frontal photographs, composite images tend towards symmetry regardless of the fluctuating asymmetries in each individual image. In order to construct composites, 172 feature points are marked on facial landmarks on each face (for details of the choice of these landmark points see Rowland & Perrett (1995)). The mean XY position of each delineated feature point is then calculated in order to generate shape information. An 'average' colour is generated by rendering colour information from each individual into this average shape and calculating mean RGB colour values across the face set for each pixel location. A high-symmetry composite face was constructed from the shape and colour of the 15 faces with the highest rated symmetry and a low-symmetry composite face was generated from the 15 faces with the lowest rated facial symmetry (figure 3). Independent *t*-tests showed that the 15 faces in each group did not differ in any of the five sexually dimorphic measures from study 2 (all values $t < 1.25$ and all values of $p > 0.22$ with d.f. = 28). The high- and low-symmetry groups did not differ significantly in any of the other physical traits measured (height, weight and body mass index).

Table 1. *Proportional dimorphic measurements from a sample of 66 male faces and 49 female faces*

	<i>n</i>	mean	s.e.	<i>t</i> (d.f. = 113)	<i>p</i>
eye size ((D1–D2)/2)					
female	49	39.44	0.25	7.986	0.000
male	66	37.14	0.16	—	—
lower face/face height (D8/D7)					
female	49	0.60	0.00	–4.456	0.000
male	66	0.62	0.00	—	—
cheekbone prominence (D3/D6)					
female	49	1.17	0.01	3.356	0.000
male	66	1.14	0.01	—	—
face width/lower face height (D3/D8)					
female	49	1.20	0.01	2.864	0.005
male	66	1.16	0.01	—	—
mean eyebrow height					
female	49	23.77	0.43	5.385	0.000
male	66	20.54	0.41	—	—

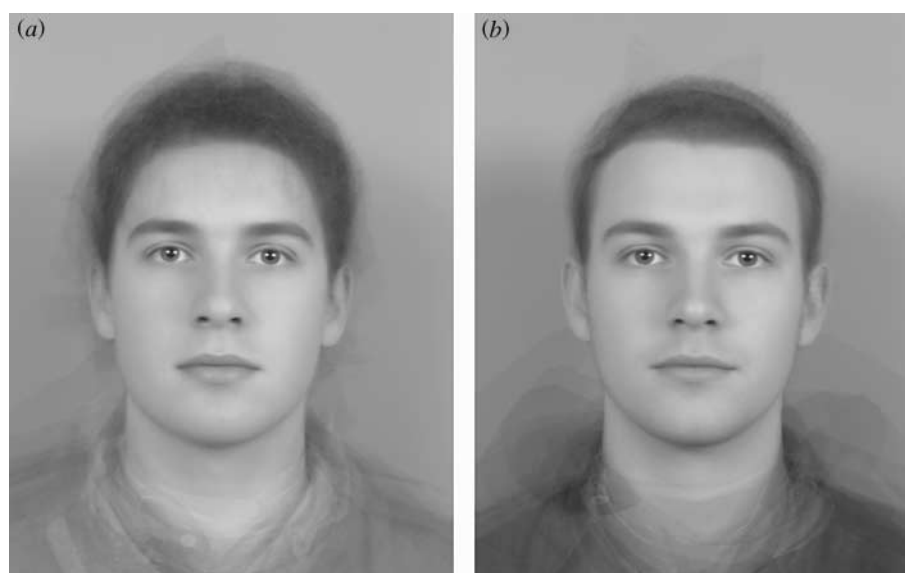


Figure 3. Composites made from 15 faces with low rated symmetry (left) and from 15 faces with high rated symmetry (right).

These two composites were presented to 77 university student raters (mean age *ca.* 22 years) who selected which was the ‘most attractive’, ‘most masculine’, ‘most physically fit’ and which had the ‘best general medical health’ using a forced-choice paradigm. Apart from 15 subjects who rated both composites for both attractiveness and masculinity, all other samples were independent.

In order to assess whether subjects were using cues from the face shape or from the hairstyles of the composites, a second set of composites were prepared that were cropped along a horizontal line bisecting the forehead. Eighty participants (mean age *ca.* 22 years) made forced-choice judgements about these faces on the same dimensions as the full-face stimuli.

3. RESULTS

(a) *Study 1*

Given the consistency of the attractiveness ratings, the mean score across raters was taken as the attractiveness for each of the 66 faces. Attractiveness was not correlated significantly with measured asymmetry ($r_s = -0.226$,

$p = 0.068$ and $n = 66$) or perceptual asymmetry ($r_s = 0.217$, $p = 0.08$ and $n = 66$). However, female raters appeared more sensitive to symmetry in male faces than male raters. When the attractiveness of each face was calculated separately from male and female ratings, both measures of symmetry were related to attractiveness for female subjects (perceptual symmetry, $r_s = 0.285$ and $p = 0.02$ and measured asymmetry, $r_s = -0.284$, $p = 0.02$ and $n = 66$), but neither measure was related to attractiveness for male subjects (perceptual symmetry, $r_s = 0.125$ and n.s. and measured asymmetry, $r_s = -0.136$, n.s. and $n = 66$).

(b) *Study 2*

In order to calculate which features are proportionally sexually dimorphic in frontal photographs *t*-tests were performed on the mean distances between points for each sex or the mean value of the ratio for each sex as appropriate (see figure 1 and table 1). In order to assess whether the significantly sexually dimorphic characteristics found in this sample (see table 2) (eye size, lower face height/face height, cheekbone prominence, face width/lower face height and mean eyebrow height) are related to either

Table 2. Responses to forced-choice comparisons of high- and low-symmetry composites in cropped and full-face conditions

(The table shows the number of subjects in each condition that selected the high-symmetry composite as being most representative of the question asked. Figures in parentheses indicate the number of female subjects. Fifteen female subjects completed full-face judgements of both attractiveness and masculinity. All other samples are independent.)

	full-face composites		cropped composites	
	<i>n</i>	picked high symmetry	<i>n</i>	picked high symmetry
attractive	20 (15)	20 (<i>p</i> = 0.00001)	20 (10)	18 (<i>p</i> = 0.0004)
masculine	30 (20)	19 (<i>p</i> = 0.10)	20 (10)	13 (<i>p</i> = 0.13)
athletic fitness	22 (11)	19 (<i>p</i> = 0.0007)	20 (10)	16 (<i>p</i> = 0.007)
medical health	20 (10)	19 (<i>p</i> = 0.00007)	20 (10)	17 (<i>p</i> = 0.002)

symmetry or attractiveness in male faces, a series of correlations were performed on each individual characteristic and an index of standardized measures.

None of the individual measured traits or ratios correlated significantly with rated symmetry (all values of $r_s < 0.23$) or measured asymmetry (all values of $r < 0.18$). None of the five dimorphic measurements were related to female-rated attractiveness (all values of $r_s < 0.21$).

Intercorrelation between the five traits was very low. Only the closely related measures of lower face height/total face height and face width/lower face height were significantly correlated ($r = -0.32$, $p = 0.008$ and $n = 66$).

An index of standardized dimorphic measures was calculated in order to provide an overall masculinity score (Z (lower face height/face height) $- Z$ (face width/lower face height) $- Z$ (eye size) $- Z$ (mean eyebrow height) $- Z$ (cheekbone prominence)). Despite the lack of correlation between each of the individual scores, this composite index correlated significantly with male judgements of male facial attractiveness ($r_s = 0.262$, $p = 0.034$ and $n = 66$). Female judgements of attractiveness also showed a trend in the same direction ($r_s = 0.209$, $p = 0.091$ and $n = 66$). However, there was no link between measured asymmetry or rated symmetry and this composite masculinity measure ($r = -0.013$ and $r_s = 0.008$, respectively, both non-significant).

(c) **Study 3**

Despite the lack of cues to symmetry in the composite image, the high-symmetry composite was rated as more attractive, more physically fit and healthier than the low-symmetry composite in both the full-face and cropped conditions. There were also trends indicating that the high-symmetry composite was judged to be more masculine than the low-symmetry composite in both conditions (table 2). As a χ^2 -test indicated that judgements of masculinity were not influenced by cropping the stimuli ($\chi^2_1 = 0.014$ and $p > 0.05$), a further binomial analysis was performed with the data collapsed across the cropped and full-face stimuli conditions and this indicated that symmetric composites were more likely to be selected as the 'more masculine' of the pair (32 out of 50 subjects) ($p = 0.016$).

4. DISCUSSION

The series of studies reported above supports several previous findings and conflicts with others and raises more questions about the role of male facial attractiveness

in signalling biological properties. Study 1 agrees with previous literature that has demonstrated preferences for symmetry in both natural and digitally manipulated facial images (Rhodes *et al.* 1998; Perrett *et al.* 1999). Humans are sensitive to asymmetries in complex naturally occurring stimuli. This sensitivity is increased when the axis of symmetry is vertical (Evans *et al.* 2000), as is the case in human faces.

However, symmetry covaries with at least one other cue in men's faces that is still visible when cues to symmetry are removed, as demonstrated by the composites generated for study 3. Our study using composites from high- and low-symmetry individuals is analogous to the half-face study reported by Scheib *et al.* (1999): the two very different techniques generate convergent findings. These results are also consistent with earlier research demonstrating that humans attend to the left side of the face more than the right side when making judgements about attractiveness, age, sex or expression (Burt & Perrett 1997).

However, the cue that covaries with symmetry is not simply related to sexual dimorphism (facial masculinity) as calculated from measurements of proportional male-female differences in two-dimensional frontal photographs. This finding conflicts with Scheib *et al.*'s (1999) finding of trait size/symmetry covariation in male faces. This discrepancy can perhaps be explained by the assumptions made by Scheib *et al.* (1999) (and others) who proposed that cheekbone prominence is a 'masculine' characteristic when, in this sample at least, it is greater in females than in males. As this measure contributes 50% of the data in Scheib *et al.*'s (1999) 'masculinity index', the conclusions of this earlier paper should be treated with caution.

Any estimates of symmetry or masculinity may be prone to measurement errors in studies of two-dimensional facial photographs. The choice of facial landmarks for both symmetry and dimorphism measurements is somewhat arbitrary, leading to the possibility that some trait size/symmetry relationships exist but remain unmeasured (e.g. inspection of figure 3 suggests that the high-symmetry composite does indeed have a more masculine hairline than the low-symmetry image). Although marking of feature points has been shown to be reliable (Grammer & Thornhill 1994; Scheib *et al.* 1999), barely perceptible lateral or vertical rotations of the head could lead to inaccurate measurements of symmetry and/or masculinity. Furthermore, both this study and the Schieb

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et al. (1999) study used proportional measures of dimorphism rather than absolute trait size. Although proportional measures lose valuable information, they do have the advantage of controlling for absolute trait size when estimating asymmetry/trait size relationships. The current study has employed perceptual measures of both symmetry and masculinity in an attempt to provide alternative estimates, but such ratings may not reflect the biological properties of the subject (cf. Meyer & Quong 1999; but see also Perrett & Penton-Voak 1999; Evans *et al.* 2000).

Clearly, however, symmetry does not appear to be the only cue to facial attractiveness in human males. Elucidating the characteristics that covary with symmetry is proving problematic. If facial symmetry is an indicator of developmental stability then one possibility is that symmetric faces also possess other cues to good health, such as a clear, unblemished complexion. This intuitive hypothesis receives some support from the data in study 3: although both composite images have unblemished skin (see Alley & Cunningham (1991) for the effects of averaging on skin texture), the high-symmetry composite is still judged as more attractive, healthier and more physically fit than the low-symmetry composite. Whilst these results could be interpreted as a psychological halo effect of attractiveness (the association of desirable characteristics with attractive faces), judgements of good health could equally be interpreted as the driving attractiveness responses (e.g. Jones *et al.* 2001a). A recent study has demonstrated that socio-economic status is the best predictor of male facial attractiveness, even when the effects of symmetry are partialled out (Hume & Montgomerie 2001). At present the nature of male attractiveness remains somewhat mysterious.

Despite the nearly complete lack of intercorrelation between individual dimorphic features found in study 2 and the lack of a relationship between these measures and symmetry, an overall masculinity index was related to men's facial attractiveness as rated by men with trends in the same direction present for females. In addition, when the two samples that had seen both cropped and full-face versions were collapsed together the high-symmetry composite was rated as more masculine than the low-symmetry composite. Although the picture is far from clear, these findings suggest that masculinity and symmetry are somewhat independent and perhaps signal different characteristics in male faces. In this sample, men consider male faces high in masculinity attractive, but symmetry has a smaller relationship with attractiveness. Women show the opposite pattern: there is a positive relationship between symmetry and attractiveness, but the composite masculinity measure does not significantly predict attractiveness. In the current study, with relatively small samples and non-parametric correlation coefficients, it is difficult to comment on the reliability of the differences between male and female raters in response to masculinity and femininity. Two other recent studies have investigated the role of sex in symmetry judgements. Little *et al.* (2001) demonstrated that women's preference for symmetry was stronger in male than in female faces. In a further study, Jones *et al.* (2001b) found a positive relationship between perceived health and symmetry in opposite-sex face stimuli for both men and women that

was weaker in same-sex judgements. In conjunction with the current study, these two findings provide a basis for speculating that preferences for symmetry may be a mate choice adaptation rather than a by-product of strategies used to process visual stimuli (e.g. Enquist & Arak 1994). It is possible that facial masculinity is more important in intrasexual competition than sexual display, with very masculine males succeeding through dominance of other males rather than female choice. However, given the high correlations between male and female ratings of attractiveness found in other studies and the relatively low sample size employed in the current study, further work is necessary in order to investigate this hypothesis.

Further complexities in the study of male facial attractiveness arise from recent findings of differences in women's preferences across time and between individuals that may represent strategic pluralism in response to social or environmental contingencies (Gangestad & Simpson 2000). Preferences for masculine traits in male faces have been demonstrated to vary across the menstrual cycle (Frost 1994; Penton-Voak & Perrett 2000) in interaction with the specific context of the attractiveness judgement ('short-' or 'long-term' relationship) and life-history factors (the presence or absence of a partner) (Penton-Voak *et al.* 1999). Women prefer relatively masculine faces in the follicular phase of their menstrual cycle, particularly when they have a long-term partner and are judging attractiveness for a short-term relationship, a finding that has implications for the role of extra-pair copulations in the evolution of human sexuality. Little *et al.* (2001) demonstrated that female self-rated attractiveness also influences preferences: women who judge themselves as more attractive prefer relatively masculine and symmetric faces, a finding that is analogous to condition-dependent mate choice in other species (e.g. Bakker *et al.* 1999). Perhaps consideration of the interactions between the properties of both the raters and multiple cues within the faces to be judged will be necessary in order to provide a fuller understanding of attractiveness judgements in our own species.

REFERENCES

- Alley, T. R. & Cunningham, M. R. 1991 Averaged faces are attractive, but very attractive faces are not average. *Psychol. Sci.* **2**, 123–125.
- Andersson, M. 1994 *Sexual selection*. Princeton University Press.
- Balmford, A., Jones, I. L. & Thomas, A. L. R. 1993 On avian asymmetry—evidence of natural-selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B* **252**, 245–251.
- Berry, D. S. & Brownlow, S. 1989 Were the physiognomists right? Personality correlates of facial babyishness. *Pers. Soc. Psychol. Bull.* **15**, 266–279.
- Berry, D. S. & McArthur, L. Z. 1985 Some components and consequences of a babyface. *J. Pers. Soc. Psychol.* **48**, 312–323.
- Berry, D. S. & Wero, J. L. F. 1993 Accuracy in face perception: a view from ecological psychology. *J. Pers.* **61**, 497–519.
- Burt, D. M. & Perrett, D. I. 1997 Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia* **35**, 685–693.
- Cunningham, M. R., Barbee, A. P. & Pike, C. L. 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.

- Enquist, M. & Arak, A. 1994 Symmetry, beauty and evolution. *Nature* **372**, 169–172.
- Evans, C. S., Wenderoth, P. & Cheng, K. 2000 Detection of bilateral symmetry in complex biological images. *Perception* **29**, 31–42.
- Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.
- Frost, P. 1994 Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. *Percept. Mot. Skills* **79**, 507–514.
- Gangestad, S. W. & Simpson, J. A. 2000 The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain Sci.* **23**, 573–644.
- 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.
- Hume, D. K. & Montgomerie, R. 2001 Facial attractiveness signals different aspects of 'quality' in women and men. *Evol. Hum. Behav.* (In the press.)
- Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001a Measured facial asymmetry and perceptual judgements of attractiveness and health. *Evol. Hum. Behav.* (Submitted.)
- Jones, B. C., Little, A. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. 2001b Evidence for an opposite-gender bias in sensitivity to symmetry when perceiving health in faces. *Evol. Hum. Behav.* (Submitted.)
- Keating, C. F. 1985 Gender and the physiognomy of dominance and attractiveness. *Soc. Psychol. Q.* **48**, 61–70.
- Kirkpatrick, M. 1996 Good genes and direct selection in the evolution of mating preferences. *Evolution* **50**, 2125–2140.
- Little, A. C., Burt, D. M., Penton-Voak, I. S. & Perrett, D. I. 2001 Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. Lond. B* **268**, 39–44.
- McArthur, L. & Apatow, K. 1983–1984 Impressions of babyfaced adults. *Soc. Cognit.* **2**, 315–342.
- McArthur, L. Z. & Berry, D. S. 1987 Cross-cultural agreement in perceptions of babyfaced adults. *J. Cross-cult. Psychol.* **18**, 165–192.
- Mazur, A., Halpern, C. & Udry, J. R. 1994 Dominant looking males copulate earlier. *Ethol. Sociobiol.* **15**, 87–94.
- Mealey, L., Bridgestock, R. & Townsend, G. 1999 Symmetry and perceived facial attractiveness. *J. Pers. Soc. Psychol.* **76**, 151–158.
- Meyer, D. A. & Quong, M. W. 1999 The bio-logic of facial geometry. *Nature* **397**, 661–662.
- Møller, A. P. 1997 Developmental stability and fitness: a review. *Am. Nat.* **149**, 916–942.
- Møller, A. P. & Hoglund, J. 1991 Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond. B* **245**, 1–5.
- Møller, A. P. & Thornhill, R. 1997 A meta-analysis of the heritability of developmental stability. *J. Evol. Biol.* **10**, 1–16.
- Møller, A. P. & 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 signaling of male quality. *Behav. Ecol.* **8**, 569–579.
- Penton-Voak, I. S. & Perrett, D. I. 2000 Female preference for male faces changes cyclically. *Evol. Hum. Behav.* **21**, 39–48.
- Penton-Voak, I. S., Perrett, D., Castles, D., Burt, M., Koyabashi, T. & Murray, L. K. 1999 Female preferences for male faces change cyclically. *Nature* **399**, 741–742.
- Perrett, D. & Penton-Voak, I. 1999 The bio-logic of facial geometry. *Nature* **397**, 662.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* **394**, 884–887.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & R., E. 1999 Symmetry and human facial attractiveness. *Evol. Hum. Behav.* **20**, 295–308.
- Petrie, M. 1994 Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.
- Rhodes, G., Proffitt, F., Grady, J. & Sumich, A. 1998 Facial symmetry and the perception of beauty. *Psychonom. Bull. Rev.* **5**, 659–669.
- Rowland, D. A. & Perrett, D. I. 1995 Manipulating facial appearance through shape and color. *IEEE Comp. Graph. Appl.* **15**, 70–76.
- Scheib, J. E., Gangestad, S. W. & Thornhill, R. 1999 Facial attractiveness, symmetry, and cues to good genes. *Proc. R. Soc. Lond. B* **266**, 1913–1917.
- Van Valen, L. 1962 A study of fluctuating asymmetry. *Evolution* **16**, 125–142.

Author: Grammer & Thornhill 1994. Is Psychol. correct expansion of Psy. in journal title?

Author: Is 2001 the correct date for Hume & Montgomerie? Also, please update if details available

Author: Is 2001 the correct date for Jones et al. (2)? Also, please update if details available.

Author: Keating 1985. Is Psychol. correct expansion of Psy. in journal title?

Author: McArthur & Berry 1987. Is Psychol. correct expansion of Psy. in journal title?

Author: Mealey et al. 1999. Is Psychol. correct expansion of Psy. in journal title?

Author: Møller 1997, Møller & Hoglund 1991 and Møller & Thornhill 1997, 1998. Change of Møller to Møller correct? As cited in the text and in other papers.

Author: Perrett & Penton-Voak 1999. This appears to be the same reference as that by Meyer & Quong. Please check and give correct details for these two references

Author: Perrett et al. 1999. Please give surname of last author in full.