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Are human preferences for facial symmetry focused on signals of developmental instability?

Leigh W. Simmons,[a] Gillian Rhodes,[b] Marianne Peters,[b] and Nicole Koehler[b]
[a]Evolutionary Biology Research Group, School of Animal Biology (M092) and
[b]School of Psychology, The University of Western Australia, Nedlands, WA 6009, Australia

Humans find symmetrical faces more attractive than are asymmetrical faces. Evolutionary psychologists claim that our preference for symmetry can be explained in the context of mate choice because symmetry is an honest indicator of the genetic quality of potential mates. These arguments assume that asymmetry in human faces is fluctuating asymmetry (FA), because this form of asymmetry can be revealing of developmental instability. However, no study has yet examined the characteristics of facial asymmetry. Here we provide the first detailed study of the patterns of asymmetry in human faces. We measured asymmetry in 35 facial traits. Although some traits had distributions characteristic of FA, many had distributions that characterize directional asymmetry (DA); on average, both men and women had right hemi-face dominance. For DA traits we used deviations from the mean asymmetry as a measure of developmental instability. Our measures of asymmetry accounted for a moderate proportion of the variance in perceived symmetry. Importantly, only FAs and random deviations from DA contributed to people's perception of symmetry. DA was not important in symmetry judgments. Faces rated as symmetrical were also rated as attractive. Random deviations from DA were weakly related to women's attractiveness judgments of men's faces. DAs did not influence attractiveness judgments. Our data suggest that people focus on aspects of facial asymmetry that may be revealing of developmental instability. Further studies that isolate FA from other forms of asymmetry are required to accurately assess the influence of developmental instability on the quality of individuals and its potential role in mate preferences. *Key words:* developmental instability, facial attractiveness, fluctuating asymmetry, humans. *[Behav Ecol 15:864–871 (2004)]*

Psychologists have long been interested in the cognitive mechanisms and adaptive significance of facial attractiveness (see Rhodes and Zebrowitz, 2002). Men and women find traits such as averageness, symmetry, and masculinity (in male) or femininity (in female) in faces attractive (for recent reviews see Fink and Penton-Voak, 2002; Thornhill and Gangestad, 1999; Zebrowitz and Rhodes, 2002). Placed in the context of sexual selection (Andersson, 1994), our preferences for facial features are proposed to be evolved adaptations for mate choice, with the targets of our preferences being signals of the genetic quality of potential mates (Thornhill and Gangestad, 1999).

Over the past decade, research on facial symmetry has been prolific, driven by the historically established link between fluctuating asymmetry (FA) and developmental instability (Mather, 1953; Van Valen, 1962; Zakharov, 1981). FA is a particular form of asymmetry characterized by random deviations from perfect symmetry in bilaterally paired traits. FA arises when an organism is unable to undergo stable development owing to environmental stress and/or genetic factors (see Polak, 2003 and references therein). FA is thus widely recognized as an outward expression of an individual's genetic quality. The study of FA has therefore had great appeal to those interested in exploring the evolution of mate preferences via sexual selection (Møller and Thornhill, 1998; Tomkins and Simmons, 2003).

Several studies have found that natural variation in facial symmetry covaries positively with perceived attractiveness (Grammer and Thornhill, 1994; Jones and Hill, 1993; Langlois et al., 1994; Mealey et al., 1999; Rhodes et al., 1998, 1999; Rikowski and Grammer, 1999; Scheib et al., 1999; Zebrowitz et al., 1996). Although experimental studies have reported both positive and negative influences of facial symmetry on attractiveness (Kowner, 1996; Swaddle and Cuthill, 1995), conflicting evidence seems mainly owing to the methods used to construct symmetric faces (Rhodes et al., 1999). Symmetric faces generated by reflecting half the face about its vertical midline are unattractive because they exaggerate structural abnormalities. Symmetric faces generated by using morphing techniques are more normal in appearance and are perceived to be more attractive than are original asymmetric versions (Perrett et al., 1999; Rhodes et al., 1998, 1999).

Given that facial symmetry is attractive to members of the opposite sex, it is tempting to conclude that facial symmetry provides a reliable cue to the genetic quality of potential mates (Gangestad et al., 1994; Grammer and Thornhill, 1994). However, the FA-sexual selection hypothesis assumes that asymmetry in human faces is FA, rather than other forms of asymmetry such as directional asymmetry (DA). DA arises owing to nonrandom genetic and/or developmental processes and, as such, may not be revealing of underlying developmental instability (Klingenberg, 2003; Palmer and Strobeck, 2003). Previous studies of facial symmetry have constructed artificial symmetry in faces, have used subjective ratings of symmetry, assuming that observed symmetry in faces is FA and therefore reflective of developmental instability, or have measured facial asymmetry without isolating FA. Although ratings of symmetry can be negatively correlated with measures of asymmetry (but see Penton-Voak et al., 2001; Rhodes et al., 2001; Scheib et al., 1999), those studies that have measured asymmetry in faces have either failed to assess its statistical properties (Grammer and Thornhill, 1994;

Address correspondence to L. W. Simmons. E-mail: lsimmons@cyllene.uwa.edu.au.
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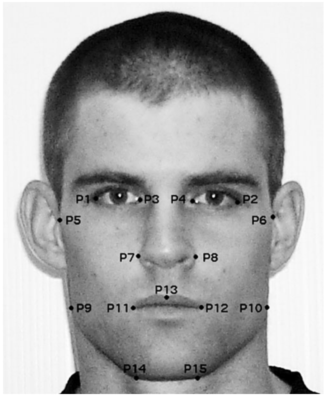

Figure 1
The location of points placed on faces for the measurement of asymmetry (see text for more details).

Penton-Voak et al., 2001; Scheib et al., 1999) or found high levels of DA with right hemi-faces being larger on average than left hemi-faces (Farkas and Cheung, 1981; Peck et al., 1991; Sackeim, 1985). One recent study that used measures of facial asymmetry and assessed their statistical properties found that significant associations between asymmetry and attractiveness held regardless of whether traits exhibiting DA were included in the composite symmetry score or not (Hume and Montgomerie, 2001). Although encouraging, this analysis does not allow us to determine the relative contributions of FA and DA to perceived facial symmetry and attractiveness, or the extent to which asymmetry in human faces reflects developmental instability.

The aim of the present study was to rigorously examine the statistical properties of asymmetry in human faces and to determine the contribution of different forms of asymmetry to perceived symmetry and attractiveness. If human preferences for symmetric faces represent an evolved strategy for mate choice based on genetic quality, as evolutionary psychologists claim, then the traits that contribute most to perceived symmetry and attractiveness should reflect underlying developmental instability.

METHODS

Subjects

Color frontal facial photographs of 172 males and 205 females with a mean age of 23.4 years (SD = 6.0, range = 18 − 47) and 22.8 years (SD = 5.5, range = 17 − 51), respectively, were used. Of these, 292 self reported themselves to be Caucasian, 73 Asian, 5 Eurasian, 2 African, 1 Australian Aboriginal, 1 New Zealand Maori, 1 Hispanic, and 1 Lebanese; one did not specify.

Facial jewelry was removed before taking photographs. Jewelry that could not be removed easily was removed on digital photographs by using the stamp tool in Adobe Photoshop, version 7.0. Occluding hair was removed from the face, shoulders, and neck region by providing participants with a headband. Subjects were asked to maintain a neutral facial expression. No males had beards. All photographs were taken under the same (symmetric) lighting conditions against a white background. Image size was controlled by taking photographs from a fixed distance (190 cm). Three facial photographs were taken of each individual, and the two best photographs (based on quality, positioning of the poser, a closed mouth, open eyes, and neutral expression) were used. All photographs were taken with a digital camera and were downloaded onto a Macintosh computer.

Ratings

One hundred eleven (54 males and 57 females) raters participated in the rating part of the study, in return for course credit, travel expenses, or as volunteers. The mean age of male and female raters was 20.3 years (SD = 4.9, range = 16–41), and 19.5 years (SD = 6.0, range = 16–55), respectively.

Adobe Photoshop was used to rotate facial photographs so that both pupil centers were located on the same y-coordinate. A black oval mask was placed individually around each face hiding most of the hair and neck, but leaving the face outline and inner hairline visible. Faces measured approximately 11.5 × 8.5 cm (height × width of oval mask) on the screen and were viewed from about 57 cm. Photographs were randomly divided into four sets: two containing 50 male and female faces, one containing 44 male and 50 female faces, and one containing 28 male and 55 female faces. The SuperLab Pro 1.75 software package was used to control the presentation order of the stimuli and record participants' responses on a Macintosh.

Participants were randomly assigned to one of two groups who rated either how symmetrical or attractive they thought each face was, using a 7-point scale (1 = not symmetrical, 7 = very symmetrical; 1 = not attractive at all, 7 = very attractive). Thus, ratings of each face's symmetry and attractiveness were independent. Participants were instructed to use the whole range of the scale if possible. For each set, the faces were blocked by sex, with order randomized within blocks, and face sex order counterbalanced with the sex of the rater for each rating set.

After participants had rated the stimuli, they were asked to indicate if they had seen any of the faces presented in the experiment before (e.g., around campus or in a previous study). Because familiarity with stimuli can influence ratings (see Hume and Montgomerie, 2001), any ratings of a face that were made by a participant who recognized that face were not included in the calculation of the average rating for that face. This involved just 0.3% of attractiveness ratings and 1.8% of symmetry ratings. Interrater reliability was good (Cronbach αs: for symmetry ratings: males rating male, 0.71, and female, 0.75, faces; females rating male, 0.63, and female, 0.72, faces. For attractiveness ratings: males rating female faces, 0.86; females rating male faces, 0.87).

For judgments of symmetry, we used the mean scores for male or female faces averaged across both male and female raters. Male ratings of symmetry correlated well with female ratings: female faces, $r = .72$, df 203, $p < .0001$, male faces, $r = .71$, df 170, $p < .0001$. However, we restricted our presentation of analyses of attractiveness to opposite sex ratings because we were interested in the potential role of symmetry in mate choice decisions.

Measurements

National Institutes of Health Image 1.62 was used to place points on landmark locations on the (unmasked) facial photographs (Figure 1). The face images were approximately 12.9 cm high (from top of hair to bottom of chin) by 9.1 cm wide (ear to ear at widest point). The screen resolution was 1024 × 768, and we used a 20-inch monitor. Corresponding points were positioned on the inside (P3 and P4) and outside (P1 and P2) corners of the eyes, cheekbones (widest horizontal part of the face below the eyes, P5 and P6), widest points at the sides of the nostrils (P7 and P8), corners of the mouth (P11 and P12), the jaw (widest horizontal part of the cheeks at the mouth, P9 and P10), and the base of the chin (P14 and P15) (Figure 1). One point was placed on the lip vertex (P13). Two of us independently positioned the points on a subset of 25 male and 25 female faces to check the reliability of the positioning of the points. There was a high reliability of positioning P1 through P15 (male faces: $r = .84$, $p < .001$; female faces: $r = .82$, $p < .001$).

Thirty-five pairwise distances between all points on the same side of the face were measured twice, once on each replicate photograph (see Appendices 1 and 2). All measurements were made in pixels. Seven of the 35 trait measures involved measuring the deviation of the bilateral points from the vertical midline. The vertical midline was calculated for each face by finding the mean midpoint of seven horizontal lines joining corresponding points on each hemi-face (i.e., P1 and P2, P3 and P4, P5 and P6, P7 and P8, P9 and P10, P11 and P12, and P14 and P15) (Figure 1). We also used these horizontal lines to calculate horizontal asymmetry, a measure of asymmetry introduced by Grammer and Thornhill (1994) and used in previous studies of face asymmetry (see Hume and Montgomerie 2001; Penton-Voak et al., 2001; Rhodes et al., 2001; Scheib et al., 1999). Briefly, horitzontal asymmetry is the sum of the deviations between the midpoints of each horizontal line and the average midpoint calculated across these lines (i.e., the vertical midline used above). In a perfectly symmetrical face, all midpoints will fall on the vertical midline.

RESULTS

A detailed statistical evaluation of the repeated measurements of asymmetry for the 35 bilaterally paired facial traits is available in Appendices 1 and 2. We analyzed male and female faces separately because faces are sexually dimorphic. In summary, for male faces all traits were significantly repeatable with a mean (±SE) F ratio of 5.52 ± 0.53, range = 2.54–15.38, df = 171,172, all $p < .001$. The mean estimate of repeatability was 0.76 ± 0.02 (range = 0.61–0.94). The same was true for female faces (mean F ratio 3.98 ± 0.32, range = 1.50–10.03, df = 204,205, all $p < .002$; mean repeatability = 0.70 ± 0.02, range = 0.52–0.90). For male faces 12 of 35 traits (34%) had the statistical properties characteristic of FA; mean values were normally distributed about zero (Appendix 1). The remaining 66% of traits exhibited DA. Five of these traits were significantly larger on the left hemi-face and 18 were significantly larger on the right hemi-face (binomial test $p = .005$), indicating that in general the population showed right facial dominance. For female faces seven of 35 traits (20%) had the statistical properties of FA (Appendix 2). Of the remaining directionally asymmetrical traits, seven were significantly larger on the left hemi-face and 21 were significantly larger on the right hemi-face (binomial test $p = .006$), again indicating right facial dominance. The difference in the proportion of traits exhibiting FA between males and females was not significant ($\chi^2_1 = 1.16$, $p = .285$).

The recommended method for determining whether asymmetry in bilateral traits conforms with a populationwide pattern of FA or DA is potentially problematic because it depends on acceptance of the null hypothesis that the mean asymmetry is equal to zero. As such, the tests are dependent on statistical power. Among other things, distinction between FA and DA will depend on sample size. With large sample sizes, very small directional asymmetries may be statistically significant even though they have no biological impact. The question of biological significance is therefore relevent here (Colegrave and Ruxton, 2003). To address this issue, we calculated Cohen's (1988) standardized effect sizes (d) and their 95% confidence bands (see Appendices 1 and 2). For male faces the effect sizes for traits accepted as showing DA ranged from 0.156–0.539, with a mean of 0.323 ± 0.026. For the smallest effect size, we could reject an effect size smaller than 0.096 and larger than 0.215 at the 2.5% level. For female faces the effect sizes for traits accepted as showing DA ranged from 0.162–0.500, with a mean of 0.333 ± 0.023. For the smallest effect size, we could reject an effect size smaller than 0.102 and larger than 0.223 at the 2.5% level. These effect sizes suggest that the traits for which we reject the null hypothesis of FA have biologically relevant levels of DA. On the other hand, with our sample size we have the power to detect deviations from zero as low as 0.15 SD units so that any traits misclassified as FA in our tests will have DA so low in effect size that they are unlikely to have biological significance, or impact, on our analyses.

From those traits found to show FA, we calculated a composite measure for each individual (FA17 in Palmer and Strobeck, 2003). We first scaled for trait size by dividing the unsigned value of FA by mean trait size, then summed FAs across traits, and divided by the total number of traits in the composite. Composite FA is thus a unitless measure and was natural log transformed to achieve normality. When we refer to FA in an individual's face, we mean the facewide asymmetry variance in those traits having populationwide patterns of FA. A composite score for DA was also calculated. We first scaled for trait size by dividing the signed value of DA by mean trait size, then summed DAs across traits, and divided by the total number of traits in the composite. When we refer to DA in faces we therefore mean the face's average side dominance calculated across all facial traits with population patterns of DA. There was no difference between males and females in composite facial FA because this score controlled for the numbers of traits with populationwide properties of FA ($t_{375} = 0.15$, $p = .879$; untransformed mean composite FA: males, 0.034 ± 0.001, females, 0.035 ± 0.001). However, because males tended to have more traits with FA, the total facial FA across traits was greater for male faces ($t_{375} = 11.12$, $p < .0001$; untransformed mean total FA: males, 0.407 ± 0.014; females, 0.244 ± 0.009). Male faces also had greater DA than did female faces, even when contrasting composite DA ($t_{375} = 2.22$, $p = .027$; untransformed mean composite DA: males, 0.009 ± 0.001; females, 0.005 ± 0.001). Levels of composite FA were not significantly associated with levels of composite DA (male faces: $r = -.13$, df = 171, $p = .081$; female faces: $r = -.08$, df = 204, $p = .250$).

Although Palmer and Strobeck (2003) suggest that as a general rule DA should be excluded from FA analyses, it has also been argued that DA and FA can both be revealing of underlying developmental instability (see Graham et al., 1993). The mean DA in a sample will not reflect the morphological outcome of random perturbations owing to developmental noise and is therefore fundamentally different from FA (Klingenberg, 2003). However, there could be random deviations about the mean DA that are owing to developmental instability (Palmer and Strobeck, 2003). We therefore used Graham et al.'s (1998) major axis technique to calculate estimates of individual asymmetry for traits showing population properties of DA. Briefly, a principle components analysis of the covariance matrix between measures of left and right sides was conducted for each DA trait. Factor scores on the first principal component represent the sum of the variation in trait sizes. Scores on the second principal component represent estimates of individual asymmetry (Graham et al., 1998). Thus extracted, we calculated a composite measure of asymmetry about DA traits by summing the absolute scores across these traits and dividing by the number of DA traits in the composite. Thus, when we refer to FA about DA traits, we mean the facewide asymmetry variance about the

Table 1

Partial regression coefficients for the effects of composite facial FA, DA, and asymmetry about DA traits on symmetry perceived by male and female raters, and on attractiveness perceived by opposite sex raters

	Male faces			Female faces		
	FA	DA	FA about DA traits	FA	DA	FA about DA traits
Symmetry	-0.29 ± 0.15*	-4.06 ± 2.43	-0.48 ± 0.19†	-0.30 ± 0.13*	2.73 ± 3.37	-0.61 ± 0.18†
Attractiveness	0.39 ± 0.21	-0.41 ± 3.41	-0.55 ± 0.19‡	0.09 ± 0.16	8.28 ± 4.21	-0.30 ± 0.22

* $p \leq .05$; † $p \leq .01$; ‡ $p \leq .001$.

population mean asymmetry of traits with DA. Male faces had significantly higher levels of composite FA about DA traits than did female faces ($t_{375} = 41.69$, $p < .0001$; males, 1.01 ± 0.03; females, 0.75 ± 0.03). Moreover, levels of asymmetry in traits with FA were positively associated with the levels of FA about traits with DA (male faces: $r = .68$, df = 170, $p < .0001$; female faces: $r = .60$, df 203, $p < .0001$).

Despite the DA in faces, it was random deviations from symmetry, rather than DA, that influenced perceived symmetry (Table 1). For male faces, FA (standardized effect size = 0.148), DA (standardized effect size = 0.127), and FA about DA traits (standardized effect size = 0.267) explained 21.7% of the variance (whole model test $F_{3,168} = 6.35$, $p < .0001$) in perceived symmetry (Table 1). For female faces, FA (standardized effect size = 0.162), DA (standardized effect size = 0.057), and FA about DA traits (standardized effect size = 0.238) explained 17.4% ($F_{3,201} = 14.10$, $p < .0001$) of the variance in perceived symmetry. For both sexes the effect of composite DA was relatively weak and insignificant.

Faces rated as being symmetrical were also rated as being attractive by opposite sex raters (male faces rated by females: $r = .46$, df = 170, $p < .0001$; female faces rated by males: $r = .54$, df = 203, $p < .0001$). FA about DA traits was the strongest predictor of attractiveness of male faces to females (standardized effect sizes: FA = 0.144, DA = 0.009, FA about DA traits = 0.216) (Table 1). The whole model explained 4.5% of the variance in attractiveness ratings ($F_{3,168} = 2.15$, $p = .049$). Attractiveness of female faces to males was not significantly influenced by any of these traits (whole model test $F_{3,201} = 1.89$, $p = .131$; standardized effect sizes: composite FA = 0.043, composite DA = 0.137, asymmetry about DA traits = 0.092) (Table 1).

To examine the extent to which previous methods of measuring asymmetry contribute to perceptions of symmetry and attractiveness, we calculated Grammer and Thornhill's (1994) horizontal asymmetry for the faces in our data set. Univariate analyses showed that horizontal asymmetry was perceived as asymmetrical (male faces: $F_{1,170} = 30.28$, $p < .0001$, regression coefficient -0.63 ± 0.12, $r^2 = .151$; female faces: $F_{1,203} = 26.16$, $p < .0001$, regression coefficient -0.72 ± 0.14, $r^2 = .114$) but did not predict attractiveness (male faces: $r^2 = .002$, $F_{1,170} = 0.39$, $p = .535$; female faces: $r^2 = .006$, $F_{1,203} = 1.18$, $p = .278$). Entering horizontal asymmetry into the analyses reported in Table 1 showed that for both male and female faces, horizontal asymmetry made relatively weak and insignificant contributions to peoples perceptions of asymmetry (male faces: effect size = 0.010, $F_{1,167} = 0.02$, $p = .890$; female faces: effect size = 0.067, $F_{1,200} = 0.93$, $p = .336$) or attractiveness (male faces: effect size = 0.069, $F_{1,167} = 0.82$, $p = .368$; female faces: effect size = 0.068, $F_{1,200} = 0.96$, $p = .329$). By far, the most informative measures for predicting perceptions of asymmetry and attractiveness were random deviations from the population mean DA. This may explain why some previous studies that have used horizontal asymmetry have found inconsistent relationships between measured symmetry and attractiveness for male and/or female faces (Hume and Montgomerie, 2001; Rhodes et al., 2001; Rikowski and Grammer, 1999; Shackelford and Larsen, 1997).

DISCUSSION

Our analyses revealed that human faces have significant levels of DA. In general, male and female faces showed right hemi-face dominance, a finding congruent with previous morphometric studies of faces (Farkas and Cheung, 1981; Peck et al., 1991; Sackeim, 1985). Interestingly, Nicholls et al. (1999) found that people asked to portray emotion displayed the left hemi-face (which tends to be smaller), and those asked to conceal emotion and to portray themselves as successful scientists displayed the right hemi-face (which tends to be larger), suggesting some functional significance for DA in the expression of emotion.

Despite the DA in human faces, it was asymmetry in traits that conformed to populationwide FA and random deviations from the population mean asymmetry in DA traits that made the strongest contributions to people's perceptions of symmetry. Indeed, for male and female faces the magnitude of DA had no significant impact on perceived symmetry, consistent with the finding that people adapt to consistent aspects of facial structure and notice deviations from them (Rhodes, 1996; Rhodes et al., 2003b; Webster and MacLin, 1999). Our data therefore suggest that our perception of symmetry in human faces may be tuned to traits that are revealing of developmental instability. Our measures of asymmetry only captured around 20% of the variance in perceived symmetry. Measures were taken from two-dimensional photographs of a complex morphological trait. People, on the other hand, are face experts and can make extremely fine discriminations between faces (Kanwisher, 2000; Peterson and Rhodes, 2003) and can detect tiny deviations from perfect symmetry about a vertical axis in complex biological images such as faces (Evans et al., 2000). It is not surprising, therefore, that we were only able to capture a small proportion of the variance in their perceptions of symmetry with our measurements. Accordingly, although perceived symmetry was strongly related to attractiveness for both male and female faces, measured asymmetry was only related to attractiveness in male faces. Interestingly, however, it was again asymmetry variance about DA that strongly influenced women's perceptions of attractiveness in men's faces, rather than the degree of DA itself. These results suggest that we can perceive subtle asymmetries that are thought to reflect underlying developmental instability, and that these perceptions can influence our judgments of attractiveness. More precise multidimensional assessments of FA might yield stronger direct relationships between FAs and attractiveness.

Males tended to have more traits that exhibited FA than did females, resulting in quantitatively more FA in male than in female faces. Furthermore, males also had greater asymmetry variance around DA traits than did females. That correlations between these two measures of asymmetry were strong and positive lends support to the notion that they both reflect the same underlying developmental instability. The sexual dimorphism is of interest because males could be more susceptible to stress during facial development than are females. During development, testosterone results in the masculinization of male faces; males develop larger jaws, chins, and prominent brow ridges (Enlow, 1990; Silvera et al., 1992; Tanner, 1978). But testosterone also suppresses the immune system (Alexander and Stimson, 1988; Grossman, 1985), perhaps exposing males to greater health-related stress during adolescence. Thus, male faces might be more susceptible to the developmental instability that generates random deviations from symmetry or DA. If both masculinity and FA signaled underlying genetic quality, we should expect men able to produce highly masculine faces to also have lower levels of FA, and females to prefer a combination of these traits. Masculinity in male faces has been shown to contribute to attractiveness in some studies (Grammer and Thornhill, 1994; Johnstone et al., 2001; Penton-Voak et al., 1999) but not others (Perrett et al., 1998; Rhodes et al., 2000; Swaddle and Reierson, 2002). The evidence for a relationship between masculinity and symmetry is equally conflicting (Gangestad and Thornhill, 2003; Penton-Voak et al., 2001; Scheib et al., 1999). The problem with the latter studies is that they consider symmetry in general, rather than FA in particular, and must therefore remain equivocal. Elsewhere we have found that masculinity is not related to FA, or any other measure of asymmetry, in our sample of male faces (Koehler et al., 2004).

Given that human faces do exhibit FAs and that FAs influence our perceptions of symmetry in faces, it is interesting to ask whether facial FA reflects the phenotypic and/or genetic quality of individuals. Body asymmetry has been suggested as a possible measure of developmental instability in humans (Livshits and Kobyliansky, 1991), and body FA is associated with poor semen quality in men (Firman et al., 2003; Manning et al., 1998). A recent meta-analysis suggests a weak effect size of general facial attractiveness on mental (0.16, 95% CI = 0.09/0.23 from 19 studies) and physical health (0.38, 0.24/0.53 from five studies; Langlois et al., 2000), and facial asymmetry is perceived as healthy (Jones et al., 2001; Rhodes et al., 2001). However, only three studies have examined the specific relationship between facial symmetry and health, and none have isolated the effect of FA. Shackelford and Larson (1997) reported more than a thousand correlations between facial symmetry and physical, psychological, and emotional health, but the number significant did not exceed that expected by chance alone. Rhodes et al. (2001) found no relation between facial symmetry of subjects and their current health or childhood, adolescent, or mid-life health. In the later data set, facial averageness, also perceived as attractive, was associated with health (Rhodes et al., 2001), and men with masculine faces had better health during adolescence (Rhodes et al., 2003a). These data therefore suggest that although some facial traits may signal health, symmetry may not be one of them. Finally, by using a combined asymmetry score that included both FA and DA, Hume and Montgomerie (2001) found that body mass index, reported health problems, or socioeconomic status were not associated with facial symmetry in males, and in females only body mass index showed a positive association. These findings did not differ qualitatively when only traits showing FA were used. Collectively, these studies provide little support for the notion that facial FA is reflective of health. Nevertheless, the costs of developmental instability may lie elsewhere, such as in longevity and/or fecundity. Recent work suggests that facial attractiveness is associated with longevity (Henderson and Anglin, 2003). Future studies need to both isolate FA in morphological traits and to see how asymmetry in these traits influences fitness in a broad life-history context.

Appendix 1

Repeatability and statistical properties of left-right measurements from male faces

	Repeatability			Statistical properties of signed left-right measures[b]								
Trait[a]	$F_{171,172}$	p	R	Mean	SD	Normality (K-S d)	Skewness	Kurtosis	$H_0 = 0$ (t_{171})	p	Effect size	95% CI for effect size
P1,2−M	10.642	.0001	0.906	−0.295	5.057	0.056	0.272	0.239	−0.765	.4456	0.058	0.022, 0.095
P3,4−M	14.194	.0001	0.930	0.743	5.495	0.064	0.177	0.333	1.773	.0780	0.135	0.080, 0.191
P5,6−M	3.818	.0001	0.738	2.874	5.431	0.051	−0.306	0.333	6.939	.0001	0.529	0.420, 0.639
P7,8−M	5.094	.0001	0.804	−0.167	4.667	0.076	0.403	0.856	−0.469	.6397	0.036	0.007, 0.064
P9,10−M	4.805	.0001	0.792	1.226	6.332	0.059	−0.359	1.593	2.539	.0120	0.194	0.127, 0.260
P11, 12−M	4.400	.0001	0.773	−2.635	4.885	0.058	−0.150	−0.297	−7.075	.0001	0.539	0.429, 0.650
P14, 15−M	8.054	.0001	0.876	−1.745	8.442	0.058	−0.508	2.095	−2.712	.0074	0.207	0.138, 0.275
P1−3, P2−4	3.267	.0001	0.694	−1.024	2.569	0.042	0.023	−0.453	−5.227	.0001	0.399	0.304, 0.494
P15, P2−6	2.540	.0001	0.606	2.982	5.737	0.035	−0.360	0.713	6.816	.0001	0.520	0.411, 0.628
P1−7, P2−8	6.865	.0001	0.854	0.488	4.064	0.056	0.268	−0.289	1.575	.1172	0.120	0.068, 0.172
P1−9, P2−10	5.872	.0001	0.830	1.305	3.996	0.052	0.028	0.488	4.283	.0001	0.327	0.241, 0.413
P1−11, P2−12	15.379	.0001	0.935	1.620	4.321	0.033	0.131	−0.176	4.917	.0001	0.375	0.283, 0.467
P1−13, P2−13	8.599	.0001	0.884	1.096	4.527	0.042	0.076	0.235	3.176	.0018	0.242	0.168, 0.316
P1−15, P2−15	8.001	.0001	0.875	0.585	3.567	0.070	0.483	3.358	2.151	.0329	0.164	0.103, 0.225
P3−5, P4−6	3.911	.0001	0.744	2.073	6.996	0.044	−0.454	0.805	3.886	.0001	0.296	0.214, 0.378
P3−7, P4−8	2.727	.0001	0.633	0.230	2.154	0.076	0.239	0.225	1.400	.1632	0.107	0.058, 0.159
P3−9, P4−10	5.362	.0001	0.814	0.710	5.235	0.071	−0.409	1.528	1.779	.0770	0.136	0.080, 0.191
P3−11, P4−12	4.629	.0001	0.784	0.219	2.458	0.036	−0.189	0.065	1.168	.2444	0.089	0.044, 0.134
P3−13, P4−13	5.909	.0001	0.831	0.493	2.637	0.041	−0.157	−0.068	2.454	.0151	0.187	0.122, 0.252
P3−14, P4−15	3.653	.0001	0.726	−0.118	1.783	0.074	−1.695	11.643	−0.871	.3851	0.066	0.027, 0.105
P5−7, P6−8	3.999	.0001	0.750	2.851	8.404	0.048	−0.452	1.065	4.450	.0001	0.339	0.252, 0.427
P5−9, P6−10	1.727	.0002	0.421	0.571	4.941	0.037	0.166	0.246	1.516	.1314	0.116	0.064, 0.167
P5−11, P6−12	3.652	.0001	0.726	3.882	7.362	0.055	−0.043	0.427	6.915	.0001	0.527	0.418, 0.637

Appendix 1, continued

Trait[a]	Repeatability $F_{171,172}$	p	R	Statistical properties of signed left-right measures[b] Mean	SD	Normality (K-S d)	Skewness	Kurtosis	$H_0 = 0$ (t_{171})	p	Effect size	95% CI for effect size
P5−13, P6−13	3.604	.0001	0.723	3.744	8.503	0.059	−0.427	0.742	5.775	.0001	0.440	0.340, 0.540
P5−14, P6−15	3.266	.0001	0.694	1.855	6.591	0.065	−0.335	2.164	3.690	.0003	0.281	0.201, 0.361
P7−9, P8−10	4.553	.0001	0.780	1.265	8.117	0.072	−0.481	2.122	2.044	.0425	0.156	0.096, 0.215
P7−11, P8−12	3.140	.0001	0.682	−0.092	2.215	0.061	−0.234	0.388	−0.543	.5877	0.042	0.010, 0.072
P7−13, P8−13	2.616	.0001	0.618	0.635	2.333	0.049	−0.278	0.285	3.567	.0005	0.272	0.194, 0.351
P7−14, P8−15	2.679	.0001	0.627	−0.349	1.948	0.049	−0.305	0.951	−2.346	.0201	0.179	0.115, 0.243
P9−11, P10−12	3.742	.0001	0.733	3.860	8.817	0.063	0.019	0.619	5.742	.0001	0.438	0.338, 0.537
P9−13, P10−13	3.809	.0001	0.737	3.254	10.245	0.049	−0.453	1.102	4.166	.0001	0.318	0.233, 0.402
P9−14, P10−15	4.183	.0001	0.761	1.526	7.003	0.080	−0.150	0.968	2.857	.0048	0.218	0.148, 0.288
P11−13, P12−13	3.181	.0001	0.686	−0.432	3.983	0.040	−0.125	−0.190	−1.423	.1565	0.108	0.059, 0.158
P11−14, P12−15	5.872	.0001	0.838	−0.855	2.922	0.034	0.079	−0.434	−0.3838	.0002	0.293	0.211, 0.374
P14−13, P15−3	15.379	.0001	0.774	0.174	2.295	0.080	−0.434	1.490	0.996	.3205	0.076	0.034, 0.117

[a] See Figure 1 for point locations.

[b] Left and right side of image so that a +ve value reflects a larger trait size on the subjects right hemiface; M = midline, R = repeatability estimate, K-S d = Kolmogorov-Smirnov test for normality.

Appendix 2

Repeatability and statistical properties of left-right measurements from female faces

Trait[a]	Repeatability $F_{171,172}$	p	R	Statistical properties of signed left-right measures[b] Mean	SD	Normality (K-S d)	Skewness	Kurtosis	$H_0 = 0$ (t_{171})	p	Effect size	95% CI for effect size
P1,2−M	7.308	.0001	0.863	−0.657	4.048	0.043	0.146	−0.364	−2.324	.0211	0.162	0.102, 0.223
P3,4−M	6.188	.0001	0.838	0.662	4.030	0.032	0.096	0.086	2.353	.0196	0.164	0.103, 0.225
P5,6−M	2.919	.0001	0.657	2.306	5.104	0.026	0.050	0.204	6.469	.0001	0.452	0.351, 0.553
P7,8−M	3.337	.0001	0.700	0.333	4.465	0.046	0.366	1.407	1.068	.2867	0.075	0.034, 0.116
P9,10−M	3.199	.0001	0.687	1.275	5.199	0.044	−0.184	−0.249	3.510	.0006	0.245	0.171, 0.320
P11, 12−M	4.353	.0001	0.770	−2.018	4.153	0.058	0.363	0.414	−6.958	.0001	0.486	0.381, 0.591
P14, 15−M	7.676	.0001	0.870	−1.901	6.958	0.041	0.029	0.288	−3.912	.0001	0.273	0.195, 0.352
P1−3, P2−4	2.075	.0001	0.518	−1.265	2.192	0.041	−0.097	−0.440	−8.263	.0001	0.577	0.463, 0.691
P1−5, P2−6	2.339	.0001	0.573	3.117	5.370	0.031	0.120	−0.033	8.311	.0001	0.580	0.466, 0.695
P1−7, P2−8	5.045	.0001	0.802	0.438	3.640	0.044	−0.005	0.133	1.724	.0862	0.120	0.068, 0.173
P1−9, P2−10	4.069	.0001	0.754	1.592	3.182	0.050	−0.124	−0.087	7.164	.0001	0.500	0.394, 0.607
P1−11, P2−12	10.026	.0001	0.900	1.555	3.888	0.033	−0.002	−0.150	5.725	.0001	0.400	0.305, 0.495
P1−13, P2−13	6.007	.0001	0.834	0.972	4.114	0.047	0.097	0.419	3.384	.0009	0.236	0.163, 0.309
P1−15, P2−15	4.346	.0001	0.770	0.819	2.744	0.047	−0.018	0.340	4.273	.0001	0.298	0.216, 0.381
P3−5, P4−6	2.476	.0001	0.596	1.739	6.358	0.042	0.103	−0.001	3.917	.0001	0.274	0.195, 0.352
P3−7, P4−8	3.097	.0001	0.677	0.825	1.924	0.062	0.328	0.257	6.139	.0001	0.429	0.330, 0.527
P3−9, P4−10	3.139	.0001	0.681	0.951	4.368	0.031	−0.070	−0.043	3.116	.0021	0.218	0.147, 0.288
P3−11, P4−12	6.748	.0001	0.852	0.457	2.586	0.031	−0.076	−0.023	2.530	.0122	0.177	0.113, 0.240
P3−13, P4−13	5.657	.0001	0.823	0.730	2.287	0.043	0.029	1.093	4.569	.0001	0.319	0.234, 0.404
P3−14, P4−15	2.664	.0001	0.625	0.118	1.327	0.049	0.010	0.594	1.269	.2059	0.089	0.044, 0.133
P5−7, P6−8	2.417	.0001	0.586	1.920	7.749	0.059	−0.334	1.371	3.547	.0005	0.248	0.173, 0.323
P5−9, P6−10	1.502	.0019	0.334	0.323	4.243	0.072	−0.420	0.445	1.090	.2770	0.076	0.035, 0.118
P5−11, P6−12	2.610	.0001	0.617	2.931	6.382	0.039	−0.110	0.278	6.575	.0001	0.459	0.357, 0.561
P5−13, P6−13	2.442	.0001	0.591	2.885	7.881	0.037	−0.099	0.303	5.242	.0001	0.366	0.275, 0.457
P5−14, P6−15	2.104	.0001	0.525	1.613	5.283	0.050	−0.164	0.722	4.372	.0001	0.305	0.222, 0.388
P7−9, P8−10	2.705	.0001	0.630	0.721	6.891	0.045	−0.345	0.457	1.498	.1357	0.105	0.056, 0.153
P7−11, P8−12	2.685	.0001	0.628	−0.553	2.126	0.045	0.145	−0.069	−3.725	.0003	0.260	0.183, 0.337
P7−13, P8−13	4.255	.0001	0.765	0.522	2.587	0.036	−0.076	−0.137	2.889	.0043	0.202	0.134, 0.269
P7−14, P8−15	3.600	.0001	0.722	−0.690	1.802	0.067	−0.830	2.372	−5.479	.0001	0.383	0.290, 0.475
P9−11, P10−12	3.139	.0001	0.681	3.293	7.558	0.064	−0.214	0.173	6.237	.0001	0.436	0.336, 0.535
P9−13, P10−13	2.699	.0001	0.630	2.831	9.126	0.047	−0.170	0.120	4.442	.0001	0.310	0.226, 0.394
P9−14, P10−15	3.717	.0001	0.731	1.820	5.876	0.022	0.038	0.000	4.434	.0001	0.310	0.226, 0.393
P11−13, P12−13	2.302	0.0001	0.566	−0.335	3.798	0.038	−0.029	−0.266	1.261	.2086	0.088	0.043, 0.133
P11−14, P12−15	5.735	.0001	0.826	−0.748	2.962	0.048	−0.110	0.082	−3.617	.0004	0.253	0.177, 0.328
P14−13, P15−13	4.626	.0001	0.784	−0.205	2.296	0.050	−0.513	1.554	−1.281	.2016	0.089	0.044, 0.134

[a] See Figure 1 for point locations.

[b] Left and right side of image so that a +ve value reflects a larger trait size on the subjects right hemiface; M = midline, R = repeatability estimate, K-S d = Kolmogorov-Smirnov test for normality.

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