

# Asymmetry and human facial attractiveness: symmetry may not always be beautiful

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## SUMMARY

It has been postulated that levels of fluctuating asymmetry in human faces may be negatively related to components of fitness such as parasite-resistance; hence potential mates with low levels of asymmetry may appear more attractive. However, previous investigations of the relationship between asymmetry and facial attractiveness have confounded manipulations of asymmetry with facial 'averageness' and mean trait size. In this experiment we performed a manipulation that altered asymmetry within a face without altering the mean size of facial features. These faces were then rated on attractiveness. Contrary to what was predicted, faces that were made more symmetrical were perceived as being less attractive. These results do not support the hypothesis that attractiveness is related to low levels of fluctuating asymmetry. The observed positive relationship between asymmetry and facial attractiveness may be because certain facial features (including those contributing to attractiveness) in fact show directional asymmetry or antisymmetry. Our manipulations thus render naturally asymmetric features symmetrical. This may make symmetric faces less attractive because of the reduction of natural directional asymmetries, perhaps making the faces appear unemotional. The role of fluctuating asymmetries alone in assessments of facial beauty is still unknown, although this experiment suggests fluctuating asymmetry is relatively unimportant compared with directional asymmetry.

## 1. INTRODUCTION

It is only recently that researchers have returned to the question of the underlying basis of perception and establishment of human physical attractiveness (Thanakar & Iwakawi 1979; Bernstein *et al.* 1982; Maret 1983; Maret & Harling 1985; Alley & Hildebrandt 1988; Buss 1989; Cunningham *et al.* 1990; Thornhill & Gangestad 1993; Grammer & Thornhill 1994; Perrett *et al.* 1994). Recent theories have proposed that human attractiveness is centred around choices for individuals that are best at resisting pathogen and parasite infection (see Thornhill & Gangestad 1993). It is possible that more heterozygous individuals are more capable of resisting infection than homozygotes, as pathogens are generally least adapted to the proteins produced by rare alleles that appear relatively more frequently in heterozygotes. If heterozygotes are better at avoiding infection they may be preferred as a mate, as they are more likely to produce viable offspring and be better able to provide parental care. In this scenario, female choice for heterozygous males could evolve under parasite-driven frequency-dependent selection (for discussion, see Mitton 1993).

There is substantial evidence that links heterozygosity with increased developmental homeostasis and low levels of fluctuating asymmetry (FA: small, random deviations from perfect symmetrical development, see Van Valen 1962). It would appear that human heterozygotes can buffer themselves against

developmental perturbations more effectively than homozygotes, and so generate morphological structures that are more symmetric (for example, see Adams & Niswander 1967; Bailit *et al.* 1970; Woolf & Gianas 1976, 1977; Townsend & Brown 1980; Soulé & Couzin-Roudy 1982; Smith *et al.* 1983; Livshits & Kobylansky 1985, 1987). Generally, because heterozygosity may be revealed by FA values, females could preferentially choose symmetric males that are more likely to be heterozygous and more capable of resisting parasitic infection. There is some zoological evidence to suggest that females prefer males that are more heterozygous (Watt *et al.* 1986) and symmetric (Møller 1992, 1993; Swaddle & Cuthill, 1994*a, b*; Swaddle 1995).

Recent theories propose that development of testosterone-mediated structures honestly advertise pathogen resistance capabilities of individuals, as only the highest quality individuals can afford the handicap of compromising their immune system by growing such structures (Fölstad & Karter 1992; Wedekind 1992). The developmental stress imposed in growing exaggerated secondary sexual traits can lead to substantially higher levels of FA in these traits than in other morphological features (Møller & Höglund 1991), with high quality individuals capable of growing both large and symmetrical display traits. Therefore, mean size and asymmetry of secondary sexual traits may both be used in mate choice (Møller 1992, 1993). Testosterone promotes the development of many

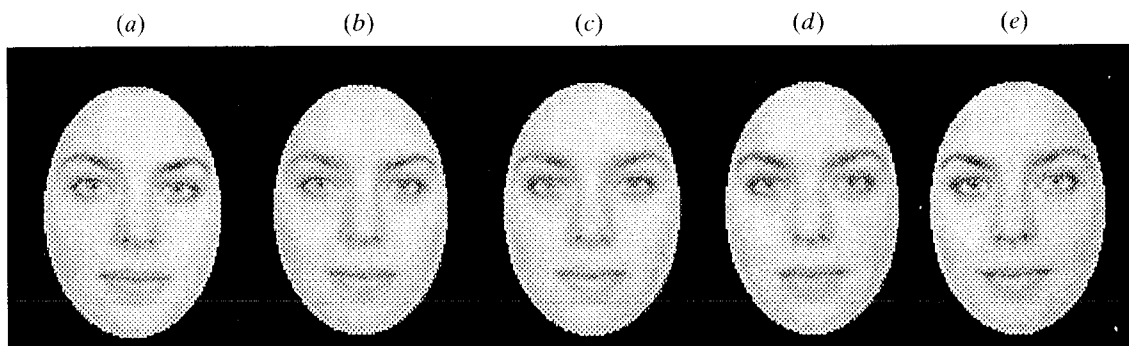


Figure 1. Example of the manipulations produced in a female face. (a) Normal; (b) NsymmI; (c) Symm; (d) NsymmII; and (e) Mirror.

secondary sexual traits in vertebrates, which should honestly reveal aspects of individual fitness. Many human facial features undergo testosterone-mediated development, especially in males (Tanner 1978; Enlow 1990; Thornhill & Gangestad 1993). If these structures do reliably reveal quality, humans seeking potential mates should assess not only the mean size of such secondary sexual traits, but also their symmetry. Two further predictions may be made. Symmetry may be perceived as being relatively more attractive in male than female faces, as the 'testosterone hypothesis' predicts that deviations from facial symmetry should be more apparent in males. Also, females may be more sensitive to symmetry in their assessment of mates. This follows from both the presumed higher susceptibility of males to FA in testosterone-mediated facial traits, and the possible higher cost to females in making 'bad' mate-choice decisions (see Andersson 1994, or any general text on sexual selection theory).

It would appear that developmental homeostasis, measured by FA, may play a role in the assessment of human attractiveness. It has been found that subjective rankings of facial attractiveness are negatively correlated with levels of FA in seven bilateral, non-facial bodily traits (Gangestad *et al.* 1995). In another study, Grammer & Thornhill (1994) obtained preliminary findings concerning the possible role of facial asymmetry in human attractiveness. In their experiment, they blended faces of different subjects together using computer-generated imagery. The more faces that they blended together, the more 'average' and symmetric the resulting image became. In other words, effects of symmetry, facial averageness and facial trait size cannot be separated. Nonetheless, they interpreted their data in a way that suggests that there is a preference for symmetry in both male and female faces. Conversely, other recent studies, using reflection of one half of the face along the midline to create symmetrical left-left and right-right composites, have found that perfectly symmetrical faces are perceived as less attractive (Langlois *et al.* 1994; Kowner 1995). There is thus a need to resolve these differences, and to separate potentially confounding effects of averageness, mean trait size and symmetry.

In this experiment we adopted a computer-generated manipulation procedure that examines these effects by independently manipulating symmetry without altering averageness or trait size within a face. We

used a repeated measures design, where photographs are manipulated to varying degrees of symmetry, and then subjectively rated for attractiveness by subjects.

## 2. METHOD

Black and white photographs of white Zoology undergraduates aged 17-19 years-old were used in this experiment (the sitters). These photographs were all taken in similar lighting conditions, with illumination from both left and right sides to minimize any lateralization of shading. No instructions were given to the sitters as to their facial expression. All the sitters were facing directly into the camera and none of the photographs displayed intense or apparent posed expressions. Sixteen male and sixteen female photographs that represented the full spectrum of attractiveness scores (based on data from a previous study, Swaddle 1994) were selected. The photographs were scanned into a pcx file using a Hewlett-Packard ScanJet IIc scanner. Using Microsoft Paintbrush, a hollow black ellipse was drawn over the face, thereby excluding hair, ears and neck from the picture. These faces were then manipulated using Gryphon Software Corporation's Morph program (Gryphon Software Corporation 1993). This software morphs pictures together by creating a two-dimensional spatially-warped crossfade between two different images. This creates a blend of two images where the elements of each of the two pictures are transplanted to an intermediate position between them (Gryphon Software Corporation 1993; see also Perrett *et al.* 1994, who use similar techniques). By morphing a normal, unmanipulated face with its mirror image, it is possible to create a perfectly symmetric image without altering average trait size. Intermediate morphs (25% and 75%) between the normal and mirror image create faces that are increasingly symmetric, but not completely so. The photographs were manipulated to produce five different conditions: (i) normal asymmetric, Normal; (ii) nearly symmetric intermediate morph that is a 25% transformation from the normal face, NsymmI; (iii) perfectly symmetric morph, Symm; (iv) nearly symmetric intermediate morph that is 25% from the mirror face, NsymmII; (v) Mirror, in which the entire face appears as it would be reflected in a mirror (the right side appears on the left and vice versa). Hardcopies of the manipulated photographs were obtained using a LaserWriter II printer (see figure 1) at a resolution of 300 dots per inch. All the images were printed 5 cm high and 3.5 cm wide, so that all 32 pictures (16 male and 16 female) could be presented simultaneously on one 420 × 594 mm sheet. Five different sheets were prepared; every sheet consisted of one manipulation from every photograph. Every sitter appeared only once on all five sheets. The manipulations were

represented equally between the five different photograph sheets. The position of pictures on the sheets was randomized.

The subjects for this experiment were 37 male and 45 female white Stage II Zoology undergraduates at the University of Bristol. Subjects were totally unfamiliar with any of the graduates used as sitters, and took part voluntarily as part of a practical session. Subjects were randomly divided into five groups; every group received a different sheet number. Every subject had their own sheet of pictures, none of the sheets were shared. Subjects were instructed to assign each picture, in turn, a score for facial attractiveness on a scale from 1 (least attractive) to 10 (most attractive). All subjects allocated scores to all photographs, irrespective of sex. Subjects were instructed to spend approximately 10 s scoring each picture independently. This experimental design meant that each group of subjects were presented with different manipulations of each sitter, so that all manipulations of all sitters were represented equally.

After inspection of the data, analysis of the results was performed using the MANOVA procedure on spss (SPSS Incorporated 1988) using untransformed data; all residuals were normally distributed. Comparisons of the effects of the different manipulations were performed by pairwise contrasts. Two-tailed tests of significance are used throughout.

3. RESULTS

There was an overall effect of the manipulations ( $F_{4,120} = 4.44, p = 0.003$ ; see figure 2). The Normal and Mirror treatments were preferred over the Symm treatment (Normal versus Symm,  $t = 3.72, p = 0.0003$ ; Mirror versus Symm,  $t = 2.97, p = 0.004$ ), but there was no attractiveness difference between Normal and Mirror Treatments (Normal versus Mirror,  $t = -0.755, p = 0.452$ ). The Normal treatment also attained higher attractiveness ratings than both NsymmI and NsymmII pictures (Normal versus NsymmI,  $t = -1.87, p = 0.064$ ; Normal versus NsymmII,  $t = -2.36, p = 0.020$ ), although this

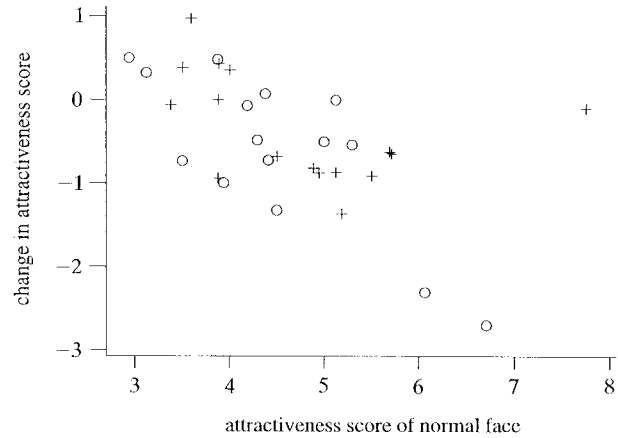


Figure 3. Correlation between the effect of symmetry manipulation (the change between Normal and Symm mean attractiveness ratings) and the mean attractiveness of each sitter. Open circles, males; crosses, females. The reduction in attractiveness of naturally attractive faces is more severe.

difference was not as large as that observed between Normal and Symm treatments. There was a tendency for NsymmI and NsymmII to be preferred over the Symm manipulation (Symm versus NsymmI,  $t = 1.85, p = 0.067$ ; Symm versus NsymmII,  $t = 1.37, p = 0.173$ ), but these differences were not significant. There was no effect of subjects' sex on attractiveness ratings (subject sex  $F_{1,30} = 0.90, p = 0.346$ ; subject sex-by-treatment interaction  $F_{4,120} = 0.46, p = 0.768$ ). Although on average female sitters were rated as more attractive than males ( $F_{1,30} = 23.91, p < 0.001$ ), there was no sitter-sex-by-treatment interaction ( $F_{4,120} = 0.62, p = 0.646$ ), nor a three-way interaction between sitter-sex, subject sex and manipulation ( $F_{4,120} = 0.18, p = 0.951$ ). That is, symmetry manipulation affected the attractiveness of both sexes, as rated by both sexes, in the same way. However, there was some evidence

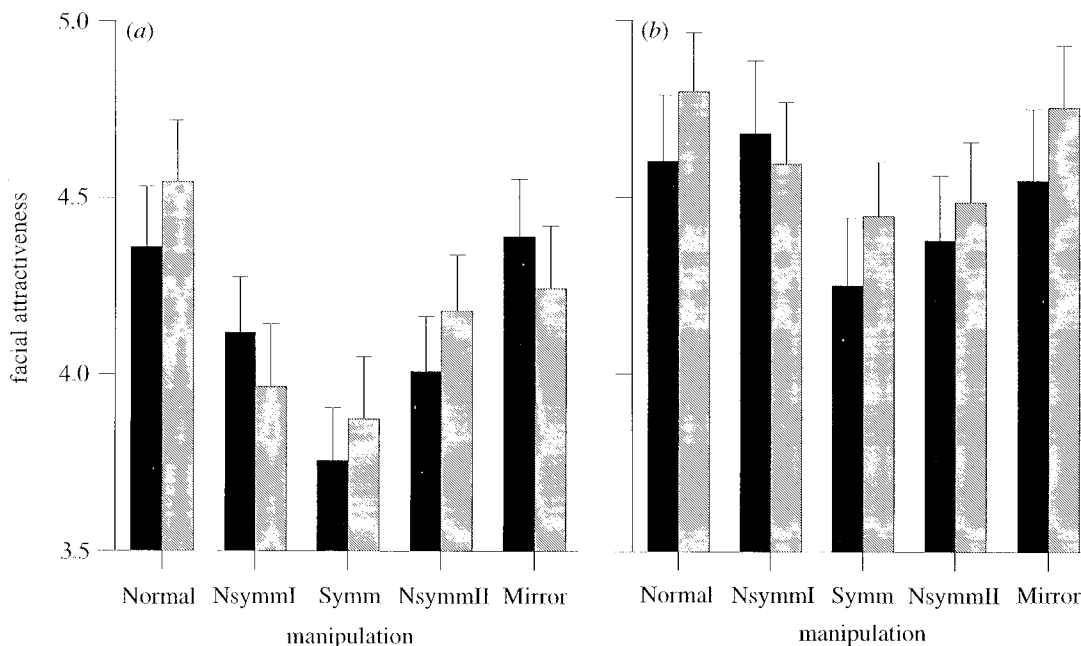


Figure 2. Mean (+ s.e.) facial attractiveness score for photographs of (a) male and (b) female sitters, as rated by male (filled bars) and female (shaded bars) subjects. There was an overall effect of the manipulations, ( $F_{4,120} = 4.44, p = 0.003$ ).

that the change in attractiveness score, as a result of increased symmetry, was greater for naturally attractive faces than less attractive ones (change in mean attractiveness, Normal–Symm, correlated with mean attractiveness of Normal: males  $r = -0.743$ ,  $p < 0.001$ ; females  $r = -0.430$ ,  $p = 0.075$ ;  $n = 16$  in each case). The only faces whose attractiveness was increased by being rendered symmetrical were those that were rated least attractive in the Normal state (see figure 3).

#### 4. DISCUSSION

These results clearly indicate that decreased facial asymmetry (NsymmI, NsymmII and Symm) is not preferred over the natural levels of asymmetry that exist in unmanipulated faces (Normal and Mirror). As asymmetry of the face decreases, perceived attractiveness of that face also decreases. This appears to be a genuine effect of the change in level of asymmetry, as the most symmetric treatment (Symm) attained the lowest scores, whereas the slightly more asymmetric treatments (NsymmI and NsymmII) received more favourable ratings (see figure 2). If the changes in attractiveness between the treatments were purely an effect of manipulation *per se*, there would be no difference between the Symm and Nsymm treatments. As the manipulations only altered facial asymmetry, and not mean trait size between the two sides of the face, we can conclude that reducing levels of asymmetry in these human faces also reduces perceived attractiveness. Facial asymmetry, at least within the natural range exhibited by our sitters, actually appears to be an attractive feature. However, this study was limited to investigations of symmetry and attractiveness in a small sample of Caucasian faces. Both the perception of symmetry and attractiveness may differ between cultures (Washburn & Crowe 1988; Perrett *et al.* 1994); therefore, it is not possible to draw conclusions concerning the general applicability of these findings across races. Nevertheless, both Langlois *et al.* (1994) and Kowner (1995) have reached similar conclusions using different procedures. Faces reflected along their midline, to produce left–left or right–right composites, were perceived as less attractive than normal faces.

The presence of a positive relationship between asymmetry and facial attractiveness does not support the parasite resistance hypothesis (Thornhill & Gangestad 1993) and conflicts with a recent experiment in which a negative relationship was found (Grammer & Thornhill 1994). Furthermore, we found no effect of sitter's (or subject's) sex on the influence of symmetry manipulation. Grammer & Thornhill's results indicated that trait averageness and symmetry were preferred in female faces, but more extreme facial traits and symmetry were preferred in male faces. However, by blending faces together to create average and symmetric faces, Grammer & Thornhill were manipulating not just trait symmetry, but also trait size and facial 'averageness'. Both trait size and facial averageness influence perceived attractiveness (Hess 1975; Terry 1977; McAfee *et al.* 1982; Berry & McArthur 1985; Cunningham 1986; Langlois &

Roggman 1990; Alley & Cunningham 1991). Therefore, in the light of our findings we would suggest that, in their study, the effect of changing levels of facial asymmetry may have been partly masked by the influence of facial averageness and trait size on attractiveness.

As part of their asymmetry analysis, Grammer & Thornhill (1994) calculated an index of asymmetry by plotting midpoints on lines that connected pairs of bilateral facial characters; they did not measure left minus right values (i.e. absolute FA, refer to Palmer & Strobeck 1986; Swaddle *et al.* 1994). They assume that on a perfectly symmetrical face, all the midpoints from several paired features would lie on the same perfectly vertical line. However, this method of assessing asymmetry does not allow for directional asymmetries acting in opposite directions in different traits, nor does it allow for the presence of antisymmetry (i.e. either the left or right component of the trait is larger, with equal probability of either) in facial features (see Van Valen, 1962 for definitions of asymmetries). Difficulties in defining the 'true' midline of a face have long been recognized in morphometrics (for example, see Sackheim & Gur 1983).

The type of manipulation performed by Grammer & Thornhill (1994), that of blending faces together, cannot isolate FA from directional asymmetry and antisymmetry. This criticism is also applicable to our manipulations, and those of Langlois *et al.* (1994) and Kowner (1995). We have decreased levels of asymmetry *per se*, not just FA; which may account for the observed positive relationship between asymmetry and attractiveness. Lowering levels of directional and antisymmetry may reduce facial attractiveness, as the human face is known to possess lateralization (i.e. asymmetry) of emotional expression (Borod & Caron 1980) and some traits may display directional asymmetries. As FAs are usually very small, the effect of reducing directional and antisymmetries may conceal any effect of FA, which may show a different relationship with attractiveness. The common feature of our study, Langlois *et al.* (1994) and Kowner (1995) is that of manipulating all asymmetries. Grammer & Thornhill's (1994) method, of blending different faces, retains directional asymmetries, but reduces them to the average of the sample.

Human faces do exhibit significant amounts of both directional asymmetry and antisymmetry in skeletal and soft tissue structures (for examples, see Farkas & Cheung 1981; Livshits & Smouse 1993). Facial asymmetries also arise due to asymmetries in muscle tone when the face is at rest (Sackheim *et al.* 1984), and directional elements of voluntary facial expression (for examples, see Campbell 1978; Ekman *et al.* 1981). Markedly reducing all asymmetries may make the face appear 'unnatural' and hence less attractive (cf. Kowner 1995). The effect that we have quantified in this experiment may not be an effect created by changing levels of FA alone. As the human face does exhibit other kinds of asymmetry than FA, there are other developmental influences acting on the face that affect perceived attractiveness. This implies that predictions concerning the role of asymmetry in

assessments of facial attractiveness that only consider FA (and not directional asymmetry and antisymmetry) are limited and, in some cases, may not be valid. It also suggests that fluctuating asymmetries will be extremely difficult to detect in human faces, as they will be hidden by the other, larger types of asymmetry. This may make the assessment of asymmetry in human faces an unreliable indicator of individual fitness (e.g. through parasite-resistance capability).

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## REFERENCES

- Adams, M. S. & Niswander, J. D. 1967 Developmental 'noise' and a congenital malformation. *Genet. Res.* **10**, 313–317.
- Alley, T. R. & Cunningham, M. R. 1991 Averaged faces are attractive, but very attractive faces are not average. *Psychol. Sci.* **2**, 123–125.
- Alley, T. R. & Hildebrandt, K. A. 1988 Determinants and consequences of facial aesthetics. In *Social and applied aspects of perceiving faces* (ed. T. R. Alley), pp. 101–140. Hillsdale, New Jersey: Erlbaum Associates.
- Andersson, M. B. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Bailit, H. L., Workman, P. L., Niswander, J. D. & MacLean, C. J. 1970 Dental asymmetry as an indicator of genetic and environmental conditions in human populations. *Hum. Biol.* **42**, 626–638.
- Bernstein, I. H., Lin, T. & McClellan, P. 1982 Cross- and within-racial judgements of attractiveness. *Percept. Psychophys.* **32**, 495–503.
- Berry, D. & McArthur, L. 1985 Some components and consequences of a baby-face. *J. pers. soc. Psych.* **48**, 312–323.
- Borod, J. C. & Caron, H. S. 1980 Facedness and emotion related to lateral dominance, sex, and expression type. *Neuropsychologia* **18**, 237–242.
- Buss, D. M. 1989 Sex differences in human mate preferences: Evolutionary hypothesis testing in 37 cultures. *Behav. Brain Sci.* **12**, 1–14.
- Campbell, R. 1978 Asymmetries in interpreting and expressing a posed facial expression. *Cortex* **14**, 327–342.
- Cunningham, M. R. 1986 Measuring the physical in physical attractiveness: Quasi-experiments in the socio-biology of female facial beauty. *J. pers. soc. Psych.* **50**, 925–935.
- 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. Psych.* **59**, 61–72.
- Ekman, P., Hager, J. C. & Friesen, W. V. 1981 The symmetry of emotional and deliberate facial actions. *Psychophysiology* **18**, 101–106.
- Enlow, D. H. 1990 *Facial growth*, 3rd edn. Philadelphia: Harcourt Brace Jovanovich.
- Farkas, L. G. & Cheung, G. 1981 Facial asymmetry in healthy North American caucasians – an anthropometrical study. *Angle Orthod.* **51**, 70–77.
- Fölstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.
- Gangestad, S. W., Thornhill, R. & Yeo, R. A. 1995 Facial attractiveness, developmental stability and fluctuating asymmetry. *Ethol. Sociobiol.* (In the press.)
- Grammer, K. & Thornhill, R. 1994 Human facial attractiveness and sexual selection: the roles of averageness and symmetry. *J. comp. Psychol.* **108**, 233–242.
- Gryphon Software Corporation 1993 *Morph user's guide*. San Diego: Gryphon Software Corporation.
- Hess, E. 1975 The role of pupil size in communication. *Sci. Am.* **233**, 110–119.
- Kowner, R. 1995 Facial asymmetry and attractiveness judgement in developmental perspective. *J. exp. Psych.: Hum. Percept. Pers.* (In the press.)
- Langlois, J. H. & Roggman, L. A. 1990 Attractive faces are only average. *Psych. Sci.* **1**, 115–121.
- Langlois, J. H., Roggman, L. A. & Musselman, L. 1994 What is average and what is not average about attractive faces. *Psychol. Sci.* **5**, 214–220.
- Livshits, G. & Kobylansky, K. 1985 Lerner's concept of developmental stability and the problem of heterozygosity levels in natural populations. *Heredity* **55**, 341–353.
- Livshits, G. & Kobylansky, K. 1987 Dermatoglyphic traits as possible markers of developmental processes in humans. *Am. J. Med. Gen.* **26**, 111–122.
- Livshits, G. & Smouse, P. E. 1993 Multivariate fluctuating asymmetry in Israeli adults. *Hum. Biol.* **65**, 547–578.
- Maret, S. M. 1983 Attractiveness ratings of photographs of blacks by Cruzans and Americans. *J. Psychol.* **115**, 113–116.
- Maret, S. M. & Harling, G. A. 1985 Cross-cultural perceptions of physical attractiveness: ratings of photos of whites by Cruzans and Americans. *Percept. Motor Skills* **60**, 163–166.
- McAfee, L., Fox, R. & Hicks, R. 1982 Attributions of male college students to variations in facial features in the line drawing of a woman's face. *Bull. Psych. Soc.* **19**, 143–144.
- Mitton, J. B. 1993 Theory and data pertinent to the relationship between heterozygosity and fitness. In *The Natural History of inbreeding and outbreeding: theoretical and empirical perspectives* (ed. N. W. Thornhill), pp. 17–41. University of Chicago Press.
- Møller, A. P. 1992 Female swallow preference for symmetrical male sexual ornaments. *Nature, Lond.* **357**, 238–240.
- Møller, A. P. 1993 Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* **32**, 371–376.
- Møller, A. P. & Höglund, J. 1991 Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond. B* **245**, 1–5.
- Palmer, A. R. & Strobeck, C. 1986 Fluctuating asymmetry: measurement, analysis and pattern. *Ann. Rev. ecol. Syst.* **17**, 391–421.
- Perrett, D. I., May, K. A. & Yoshikawa, S. 1994 Facial shape and judgements of female attractiveness. *Nature, Lond.* **368**, 239–242.
- Sackheim, H. A. & Gur, R. C. 1983 Facial asymmetry and the communication of emotion. In *Social psychophysiology: a sourcebook* (ed. J. T. Cacioppo, R. E. Petty & D. Shapiro), pp. 313–352. New York: Guilford Press.
- Sackheim, H. A., Weiman, A. L. & Forman, B. D. 1984 Asymmetry of the face at rest: size, area and emotional expression. *Cortex* **20**, 165–178.
- Smith, B. H., Garn, S. M. & Cole, P. M. 1983 Problems of sampling and inference in the study of fluctuating dental asymmetry. *Am. J. phys. Anthropol.* **58**, 281–289.
- Soulé, M. E. & Couzin-Roudy, J. 1982 Allometric vari-

- ation. 2. Developmental instability of extreme phenotypes. *Am. Nat.* **120**, 765–786.
- SPSS Incorporated 1988 *SPSSx User's guide*, 3rd edn. Chicago: SPSS Incorporated.
- Swaddle, J. P. 1994 The role of fluctuating asymmetry in sexual selection. Ph.D. thesis: Bristol University.
- Swaddle, J. P. 1995 Reproductive success and symmetry in zebra finches. *Anim. Behav.* (In the press.)
- Swaddle, J. P. & Cuthill, I. C. 1994a Preference for symmetric males by female zebra finches. *Nature, Lond.* **367**, 165–166.
- Swaddle, J. P. & Cuthill, I. C. 1994b Female zebra finches prefer males with symmetrically manipulated chest plumage. *Proc. R. Soc. Lond. B* **258**, 267–271.
- Swaddle, J. P., Witter, M. S. & Cuthill, I. C. 1994 The analysis of fluctuating asymmetry. *Anim. Behav.* **48**, 986–989.
- Tanner, J. M. 1978 *Foetus into man: Physical growth from conception to maturity*. London: Corsano.
- Terry, R. 1977 Further evidence on components of facial attractiveness. *Percep. Motor Skills* **45**, 130.
- Thanakar, J. N. & Iwakawi, S. 1979 Cross-cultural comparison in interpersonal attraction of females toward males. *J. Soc. Psych.* **108**, 121–122.
- Thornhill, R. & Gangestad, S. W. 1993 Human facial beauty: averageness, symmetry and parasite resistance. *Hum. Nat.* **4**, 237–269.
- Townsend, G. C. & Brown, T. 1980 Dental asymmetry in Australian aboriginals. *Hum. Biol.* **52**, 661–673.
- Van Valen, L. 1962 A study of fluctuating asymmetry. *Evolution* **16**, 125–142.
- Washburn, D. K. & Crowe, D. W. 1988 *Symmetries of culture*. Seattle: University of Washington Press.
- Watt, W. B., Carter, P. A. & Donohue, K. 1986 Females' choice of 'good genotypes' as mates is promoted by an insect mating system. *Science, Wash.* **233**, 1187–1190.
- Wedekind, C. 1992 Detailed information about parasites revealed by sexual ornamentation. *Proc. R. Soc. Lond. B* **247**, 169–174.
- Woolf, C. M. & Gianas, A. 1977 A study of fluctuating dermatoglyphic asymmetry in the sibs and parents of cleft lip propositi. *Am. J. Hum. Genet.* **28**, 503–507.

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