ELSEVIER

Evolution and Human Behavior 22 (2001) 417–429

Evolution and Human Behavior

Facial symmetry and judgements of apparent health Support for a "good genes" explanation of the attractiveness–symmetry relationship

B.C. Jones*, A.C. Little, I.S. Penton-Voak, B.P. Tiddeman, D.M. Burt, D.I. Perrett

School of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9AJ, Scotland, UK

Received 27 February 2001; received in revised form 11 April 2001; accepted 5 June 2001

Abstract

The "good genes" explanation of attractiveness posits that mate preferences favour healthy individuals due to direct and indirect benefits associated with the selection of a healthy mate. Consequently, attractiveness judgements are likely to reflect judgements of apparent health. One physical characteristic that may inform health judgements is fluctuating asymmetry as it may act as a visual marker for genetic quality and developmental stability. Consistent with these suggestions, a number of studies have found relationships between facial symmetry and facial attractiveness. In Study 1, the interplay between facial symmetry, attractiveness, and judgements of apparent health was explored within a partial correlation design. Findings suggest that the attractiveness–symmetry relationship is mediated by a link between judgements of apparent health and facial symmetry. In Study 2, an opposite-sex bias in sensitivity to facial symmetry was observed when judging health. Thus, perceptual analysis of symmetry may be an adaptation facilitating discrimination between potential mates on the basis of apparent health. The findings of both studies are consistent with a "good genes" explanation of the attractiveness–symmetry relationship and problematic for the claim that symmetry is attractive as a by-product of the ease with which the visual recognition system processes symmetric stimuli.

Keywords: Faces; Attractiveness; Perceived health; Mate preferences; Asymmetry

* Corresponding author. Tel.: +44-1334-46-2088; fax: +44-1334-46-3042.
E-mail address: bcj@st-andrews.ac.uk (B.C. Jones).

1090-5138/01/$ – see front matter
PII: S1090-5138(01)00083-6

1. Introduction

The "good genes" account of attractiveness posits that mate preferences may have evolved to favour healthy individuals due to direct and indirect benefits associated with the selection of a healthy mate (Andersson, 1994; Gangestad & Simpson, 2000; Miller & Todd, 1998; Thornhill & Gangestad, 1993, 1999). If this is the case, attractiveness judgements are likely to reflect judgements of health (Grammer & Thornhill, 1994). It has also been suggested that fluctuating asymmetry is a visual marker for genetic quality and developmental stability—the ability to maintain good health in the face of environmental insults (Gangestad & Simpson, 2000; Møller & Swaddle, 1997; Møller & Thornhill 1997; Thornhill & Møller, 1997).

Consistent with these suggestions, a number of studies have found that symmetry in real faces is associated with judgements of facial attractiveness (Grammer & Thornhill, 1994; Hume & Montgomerie, 2001; Mealey, Bridgestock, & Townsend, 1999; Rhodes, Proffitt, Grady, & Sumich, 1998; Rhodes, Sumich, & Byatt, 1999; Scheib, Gangestad, & Thornhill, 1999). Moreover, preferences for faces that have been "morphed" to be more symmetrical have also been reported (Perrett et al., 1999; Rhodes et al., 1998; Rhodes, Yoshikawa, et al., 2001). Consequently, many researchers have concluded that symmetry is a visual cue to facial attractiveness. For some, however, the link remains in debate (e.g., Penton-Voak et al., 2001; Scheib et al., 1999; Swaddle & Cuthill, 1995).

Both Grammer and Thornhill (1994) and Penton-Voak et al. (2001) found that judgements of health were related to symmetry in male faces. In line with these findings, Rhodes, Zebrowitz, et al. (2001) reported associations between rated facial symmetry and judgements of apparent health for both male and female faces. The apparent health of symmetric faces could, however, reflect an "attractiveness halo" where positive attributes (e.g., extraversion, stability, and good health) are ascribed to good looking, symmetrical individuals (Penton-Voak et al., 2001). Indeed, there is some evidence that apparent good health may simply be a stereotype associated with attractive individuals (Kalick, Zebrowitz, Langlois, & Johnson, 1998). If the relationship between symmetry and judgements of apparent health was mediated by an attractiveness halo effect, it would pose difficulties for a "good genes" explanation of the attractiveness–symmetry relationship (see Feingold, 1992; Langlois et al., 2000 for meta-analytic reviews of research on attractiveness halo effects).

It has been reported that manipulating digital face images so as to increase symmetry engenders an increase in ratings of apparent health (Rhodes, Zebrowitz, et al., 2001). This finding suggests that symmetry is a cue to judgements of health. If the processing of symmetry by the perceptual system is an adaptation facilitating discrimination between potential mates on the basis of apparent health (Møller & Thornhill, 1998), a strong adaptationist position might predict an opposite-sex bias in sensitivity to facial symmetry. In contrast, no such bias is predicted by accounts claiming that symmetry is found attractive as a by-product of the ease with which the recognition system can process symmetric stimuli (e.g., Bradbury & Vehrencamp, 1998; Enquist & Arak, 1998; Enquist & Ghirlanda, 1998). Consistent with the strong adaptationist position, Little, Burt, Penton-Voak, and Perrett

(2001) report that manipulations of symmetry have a greater impact on attractiveness ratings of opposite-sex faces than ratings of own-sex faces. As yet, there have been no reported tests for such a bias when judging apparent health.

Two studies are reported here that explore predictions about the relationship between facial symmetry and judgements of apparent health that arise from the "good genes" explanation of attractiveness.

2. Study 1

In Study 1, the interplay between measured facial symmetry, judgements of apparent health, and judgements of attractiveness was explored within a partial correlation design. The "good genes" explanation of attractiveness predicts that, rather than being the result of an attractiveness halo, the association between symmetry and judgements of apparent health mediates the attractiveness–symmetry relationship. Consequently, if the association between facial symmetry and apparent health judgements remains when controlling for the effects of attractiveness, the "good genes" explanation is supported. It is also supported if the attractiveness–symmetry relationship disappears when controlling for apparent health. On the other hand, if judgements of apparent health do not mediate the attractiveness–symmetry relationship, this relationship should remain when controlling for the effects of judgements of apparent health. Similarly, the null hypothesis would predict that there would be no relationship between judgements of apparent health and facial symmetry when controlling for attractiveness.

3. Method

3.1. Participants

Ten male (21–26 years old) and 10 female (20–28 years old) participants took part in Study 1. All participants reported normal or corrected-to-normal vision and were naïve to the purpose of the experiment.

3.2. Stimuli

Full-face photographs of 30 males and 30 females (20–30 years of age, all undergraduate students at the University of St. Andrews) were used. Each full-colour photo was taken with a digital camera (resolution set at 1200×1000 pixels) and under standardised diffuse lighting conditions. Background was constant in all photographs. Facial expression was neutral, hair pulled back from the face and facial adornments (e.g., jewellery or make up) removed prior to photographing. All males were clean-shaven. Images were normalised on interpupillary distance. All individuals photographed were unfamiliar to those participants who took part in the ratings phase of the study.

3.3. Measures

3.3.1. Asymmetry

Each digital face-image was first scaled and rotated so as to standardise interpupillary distance to 100 units. A horizontal axis was then created that bisected both pupil centres. A vertical axis was set perpendicular to, and bisecting, the horizontal axis. Distances between the vertical axis and each of 12 bilaterally paired points (Fig. 1) were measured parallel to the horizontal axis. These signed distances were then summed to calculate horizontal asymmetry (alternatively referred to as L−R asymmetry; Hume & Montgomerie, 2001).

Calculating facial asymmetry using horizontal asymmetries only (in line with Grammer & Thornhill, 1994; Hume & Montgomerie, 2001; Rhodes, Zebrowitz, et al., 2001), rather than combining vertical and horizontal asymmetries as other studies have done (e.g., Penton-Voak et al., 2001; Scheib et al., 1999) pays close attention to the finding that human perceivers are primarily sensitive to horizontal asymmetries in complex biological images, including faces (Evans, Wenderoth, & Cheng, 2000). It has been reported that facial metric techniques of this kind yield measurements of facial asymmetry that can be calculated with high repeatability (Hume & Montgomerie, 2001). It has also been found that facial asymmetry calculated using distance measurements from 2D images correlated significantly with perceptual measures of facial asymmetry (Rhodes, Zebrowitz, et al., 2001).

3.3.2. Attractiveness and apparent health ratings

Each participant rated all of the photographs for the attributes *attractiveness* and *health* using a Likert-type 1−7 scale (1 = *very low*, 4 = *neutral*, 7 = *very high*). Item order was fully

Fig. 1. Facial-metric technique: pairs of bilateral points used to calculate asymmetry.

randomised and the order in which attractiveness and health ratings were given was counterbalanced across participants. Photographs were 6 □ 4 cm in size and printed in 24-bit colour when presented for rating. Viewing distance was approximately 50 cm.

4. Results

4.1. Interrater reliability

Interrater agreement for ratings of both attractiveness (Cronbach's α=.83) and apparent health (Cronbach's α=.92) were higher than .8 and rating was therefore taken to be reliable (Bohrnstedt, 1970). Ratings from male and female participants were combined for subsequent analyses.

4.2. Descriptive statistics

Summary statistics of all measures are shown in Table 1. Table 1 also shows that for each measure the distribution of scores did not differ significantly from a normal distribution, and that the most extreme value for each measure (i.e., the value furthest from the mean in either direction) was not a significant outlier. Bivariate plots indicated that outliers did not cause the reported simple correlations.

4.3. Simple correlations

These results are summarised in Table 2 (all probabilities are one-tailed as the direction of the correlations was predicted on the basis of previous studies). For ratings of attractiveness, significant negative correlations with measured facial asymmetry were observed for both male faces and female faces. The slopes of these correlations did not differ significantly (Fisher *r*-to-*z* transformations: z=0.09, P=.464). Similarly, for ratings of apparent health, significant negative correlations with facial asymmetry were observed for both male and female faces. Again, the correlations did not differ significantly in slope (z=0.03, P=.464). Finally, significant positive correlations between ratings of attractiveness and apparent health

Table 1
Descriptive statistics for all measures, Kolmogorov–Smirnov test for differences from a normal distribution and Grubb's test for detecting outliers (all probabilities two-tailed)

Sex of face	Measure	Mean	S.D.	*N*	*z* (K–S)	*P* (K–S)	*Z* (Grubb's)	*P* (Grubb's)
Female	attractiveness	2.8	1.478	30	0.589	.879	2.244	> .05
Male	attractiveness	4.2	0.970	30	0.924	.360	2.860	>.05
Female	health judgements	4.0	1.196	30	0.587	.881	1.814	>.05
Male	health judgements	2.8	1.200	30	0.767	.599	2.29	>.05
Female	asymmetry	21.3	9.372	30	0.825	.504	2.825	>.05
Male	asymmetry	38.1	16.680	30	0.685	.735	2.357	>.05

Table 2
Bivariate correlations between ratings in Study 1

Sex of face presented	Correlation between	*r*	*N*
Male	asymmetry and health judgements	□ .504**	30
Female	asymmetry and health judgements	□ .510**	30
Male	asymmetry and attractiveness	□ .429***	30
Female	asymmetry and attractiveness	□ .409*	30
Male	attractiveness and health judgements	.487**	30
Female	attractiveness and health judgements	.783***	30

Male and female raters are pooled and all probabilities are one-tailed.
* Significant at .05 level.
** Significant at .01 level.
*** Significant at .001 level.

were observed for both male and female faces. In contrast to the previously reported simple linear correlations, the slopes of these associations were significantly different ($z = 1.91$, P=.042), indicating that ratings of apparent health and attractiveness were more closely related for female faces.

4.4. Partial correlations

These results are summarised in Table 3 (as for the simple linear correlations, probabilities are one-tailed as the direction of the correlations was predicted on the basis of previous studies). The correlation between ratings of apparent health and measured facial asymmetry persisted when controlling for perceived attractiveness for both male and female faces. The slopes of the two correlations did not differ significantly ($z = 0.16$, P=.44). By contrast, the association between ratings of attractiveness and measured facial asymmetry did not persist when controlling for perceived health for ratings given in response to either male faces or female faces. Finally, when controlling for the effects of asymmetry, a significant positive association between ratings of apparent health and attractiveness was

Table 3
Partial correlations between ratings in Study 1

Sex of face presented	Correlation between	Controlling for effects of	Partial *r*	*df*
Male	asymmetry and health judgements	attractiveness	□ .374*	27
Female	asymmetry and health judgements	attractiveness	□ .335*	27
Male	asymmetry and attractiveness	health judgements	□ .244	27
Female	asymmetry and attractiveness	health judgements	□ .031	27
Male	attractiveness and health judgements	asymmetry	.347*	27
Female	attractiveness and health judgements	asymmetry	.714***	27

Male and female raters are pooled and all probabilities are one-tailed.
* Significant at .05 level.
*** Significant at .001 level.

observed for both male and female faces. In this instance, the slopes of the two correlations were significantly different ($z = 1.85$, $P = .032$). As for the simple correlations, ratings of health and facial attractiveness were more closely related when judging female faces than when judging male faces.

5. Discussion

The simple linear correlations found in Study 1 show that high attractiveness is attributed to individuals whose faces are symmetrical. This finding is consistent with other studies (Grammer & Thornhill, 1994; Hume & Montgomerie, 2001; Mealey et al., 1999; Perrett et al., 1999; Rhodes et al., 1998, 1999; Rhodes, Zebrowitz, et al., 2001; Scheib et al., 1999). The simple linear correlations also show that good health is attributed to individuals whose faces are symmetrical which, again, is consistent with other studies (Grammer & Thornhill, 1994; Penton-Voak et al., 2001; Rhodes, Zebrowitz, et al., 2001).

The relationship between measured facial symmetry and ratings of apparent health remained when controlling for attractiveness. This is inconsistent with the suggestion that the association between facial symmetry and judgements of apparent health may be caused by an attractiveness halo (Penton-Voak et al., 2001), whereby symmetric and therefore attractive individuals are automatically ascribed positive attributes, including apparent good health (Feingold, 1992; Langlois et al., 2000). By contrast, the association between facial symmetry and attractiveness disappeared when controlling for the effects of judgements of apparent health. This supports the view that the attractiveness–symmetry relationship is mediated by the link between facial symmetry and judgements of apparent health and is consistent with the "good genes" explanation of attractiveness.

The slopes of the correlations between ratings of apparent health and attractiveness were significantly different for ratings of male and female faces. This indicates that the link between judgements of apparent health and attractiveness was stronger for judgements of female faces than for judgements of male faces. This effect was also observed when controlling for asymmetry. Though a "good genes" explanation of attractiveness might predict a stronger relationship between ratings of attractiveness and health for male faces than female faces (Grammer & Thornhill, 1994), the observed effect is consistent with the finding that past health problems predicted female facial attractiveness better than it predicted male facial attractiveness (Hume & Montgomerie, 2001).

6. Study 2

Study 2 explored the impact of manipulations of facial symmetry on perceived health. A strong adaptationist position would predict an increased sensitivity to facial symmetry when judging the apparent health of opposite-sex face images. Apparent health ratings of images of normal faces were compared with ratings of images of faces in which symmetry was increased by digitally "morphing" the image.

7. Method

7.1. Participants

Thirteen male (20–30 years old) and 13 female (20–30 years old) participants took part in Study 2. All participants reported normal or corrected-to-normal vision and were naïve to the purpose of the experiment. None of the participants in Study 2 had taken part in Study 1.

7.2. Design

A within-subjects design was used with factors *facial symmetry* (two levels: normal, more symmetrical) and *sex of face* (two levels: own-sex, opposite-sex).

7.3. Stimuli

Male and female faces (Caucasian, 15 male and 15 female, ages 20–30 years, posing with neutral expressions and head pointing straight at camera) were photographed with a digital camera (24-bit colour, resolution set at 531 × 704 pixels) and under standardized diffuse lighting conditions. Background was constant in all photographs. All faces were without make-up or adornments (e.g., earrings), hair was pushed back off the forehead and all males were clean-shaven. All individuals photographed were employees at a UK industrial research center and were unfamiliar to the participants in the ratings phase of the study. Images were scaled and rotated to standard pupil center positions. Two hundred and twenty-four predefined feature points were marked on each face in order to capture the distinctive shape of individual facial features while maintaining an equivalent spacing on the left and right sides of the face (Benson & Perrett, 1991; Perrett, May, & Yoshikawa, 1994; Rowland & Perrett, 1995). A more symmetrical version of each face was then created by averaging the height and lateral position (relative to a midline perpendicular to and bisecting the interpupillary line) of corresponding pairs of feature markers on the left and right sides of the face. Each digital face image was then remapped (Benson & Perrett, 1991; Perrett et al., 1994; Rowland & Perrett, 1995) into the corresponding symmetrical shape. Images were then cropped to reduce visibility of the hair and neck. Fig. 2 shows normal and more symmetrical (i.e., “morphed”) versions of a digital face image.

7.4. Procedure

Each participant rated all 60 faces for “apparent general medical health” using a 1–7 Likert-type scale (1 = *very low*, 4 = *neutral*, 7 = *very high*). Faces were randomly allocated to one of two blocks of 30 items except that in no single block was a face presented in both normal and symmetrical versions (Perrett et al., 1999). Within each block participants were free to revise ratings in light of subsequently presented items and order of presentation of

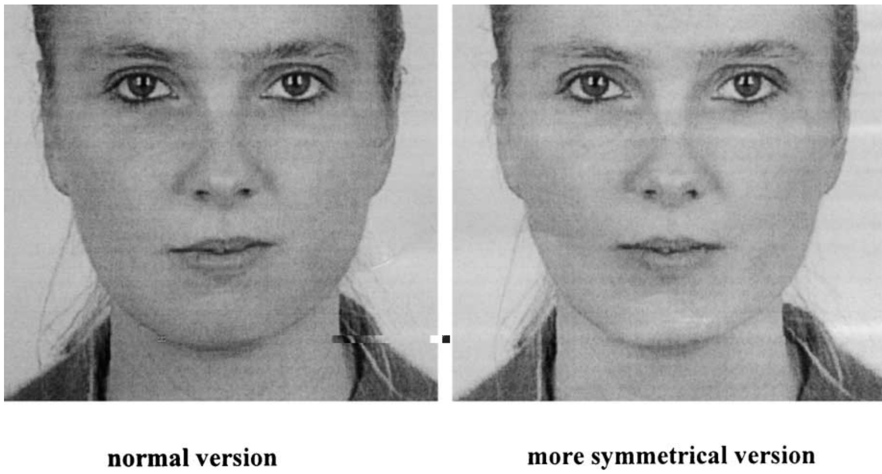

Fig. 2. Normal and more symmetrical versions of a face.

faces was fully randomised. Photographs were printed in 24-bit colour and were 6 × 4 cm in size when presented for rating. Viewing distance was approximately 50 cm.

8. Results

Mean ratings of apparent health for own-sex symmetrical, opposite-sex symmetrical, own-sex normal, and opposite-sex normal faces were calculated for each participant and used in subsequent analyses. As the distribution of ratings was not significantly different from a normal distribution (Table 4), parametric tests were used for subsequent analyses.

A within-participants analysis of variance (ANOVA) showed a significant main effect for *facial symmetry* [$F(1,103) = 114.6$, $P < .001$] and no main effect for *sex of face* [$F(1,103) = 0.4$, $P = .8$]. The significant main shows that increasing facial symmetry increased ratings of apparent health (mean rating of original face = 3.3, S.E. = 0.08; mean rating of symmetric faces = 4.4, S.E. = 0.06).

There was a significant 2 × 2 interaction (Fig. 3) between *facial symmetry* and *sex of face* [$F(1,103) = 4.2$, $P = .042$]. Further analyses showed that manipulating facial symmetry had a significant impact on health ratings for both opposite-sex [$F(1,51) = 96.2$, $P < .001$] and own-

Table 4
Kolmogorov–Smirnov tests for differences from normal distribution for ratings in Study 2

Face set	Kolmogorov–Smirnov *z*	*P*
All faces	0.897	.397
More symmetrical versions of faces	0.749	.628
Normal versions of faces	0.766	.600

Male and female raters are pooled and all probabilities two-tailed.

sex conditions [$F(1,51) = 32.4$, $P < .001$]. The difference between ratings of the original faces and ratings of the symmetrical faces was significantly more pronounced when rating opposite-sex faces than rating own-sex faces [$F(1,51) = 8.8$, $P = .005$].

9. Discussion

The observed main effect for facial symmetry shows that increasing symmetry improved ratings of apparent health. Though this link between facial symmetry and apparent health occurred when rating both own-and opposite-sex faces, analyses indicated an opposite-sex bias in sensitivity to facial symmetry when judging health (Fig. 3). This finding is consistent with the suggestion that the perceptual analysis of facial symmetry may be an adaptation facilitating discrimination between potential mates on the basis of apparent health (Møller & Thornhill, 1998). That symmetry is a *cue* to perceived health replicates the finding of Rhodes, Zebrowitz, et al. (2001) and is consistent with the *associations* between symmetry and judgements of apparent health found in Study 1.

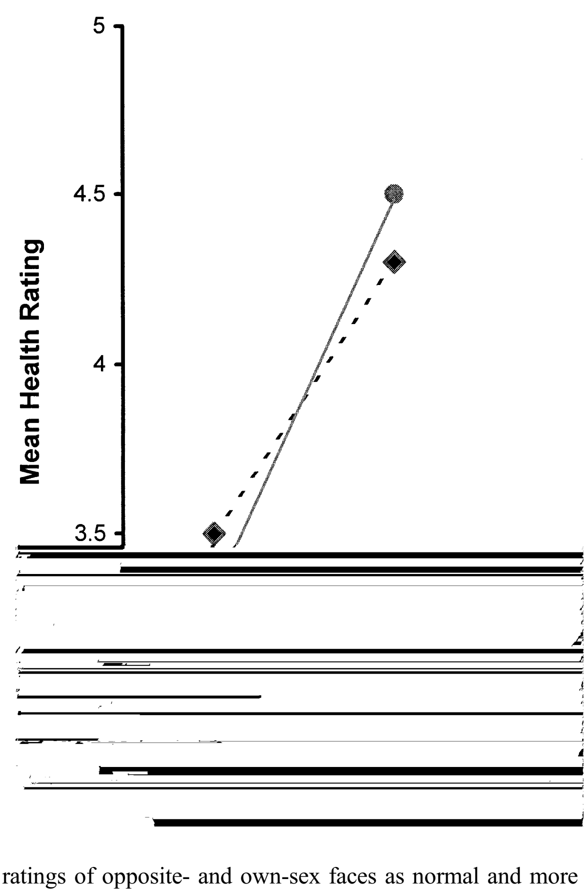

Fig. 3. Mean health ratings of opposite- and own-sex faces as normal and more symmetrical versions.

The opposite-sex bias in sensitivity to facial symmetry is consistent with the findings of Little et al. (2001) who report such a bias when judging attractiveness. The opposite-sex bias was not reported by Rhodes, Zebrowitz, et al. (2001). This may reflect the employment of a different methodology to the present study: Rhodes et al. (2001) used face images presented with either smoother skin textures in the symmetrical condition than in the asymmetrical condition or unnaturally smooth skin textures in both conditions. Consequently, the symmetric images they used may not accurately represent real faces. Study 2 used more realistic digital faces—ensuring that both symmetrical and original versions of faces were presented with the original skin textures.

10. General discussion

The findings of Study 1 indicate that the relationship between facial symmetry and attractiveness is mediated by judgements of apparent health. This is evidence against the proposition that the attractiveness of symmetry is simply a by-product of the ease with which the recognition system can process symmetric stimuli (e.g., Bradbury & Vehrencamp, 1998; Enquist & Arak, 1998; Enquist & Ghirlanda, 1998). It may be that the undergraduate population, sampled in order to create the item set in Study 1, represented a truncated range of facial asymmetry. If this was the case, sample sizes in the present study may not have been large enough to reveal weak associations. This may explain why a residual attractiveness–symmetry relationship was not observed when controlling for the effects of judgements of apparent health. Despite this caveat, it can still be concluded that judgements of apparent health contribute to the attractiveness–symmetry relationship to a greater extent than attractiveness contributes to the association between judgements of apparent health and facial symmetry.

Similarly, the claim that the attractiveness–symmetry relationship simply reflects the ease with which the recognition system can process symmetric stimuli does not predict that facial symmetry would act as a visual cue to judgements of apparent health, as was observed in Study 2. In addition to this, such an account cannot accommodate the finding that symmetry has a differential impact when judging the apparent health of opposite- and own-sex faces.

Tests for relationships between physical health and either facial attractiveness (Kalick et al., 1998) or facial symmetry (Rhodes, Zebrowitz, et al., 2001) have found no significant associations. Though Shackelford and Larsen (1999) found weak associations between facial attractiveness and physical health, these results were not replicated across their two samples and the validity of the health measures they used has been questioned (Rhodes, Zebrowitz, et al., 2001). In a similar vein, Hume and Montgomerie (2001) found associations between facial attractiveness and past health problems, though again this finding was reliant on self-reported measures of physical health. The weak and inconsistent findings on this point may appear problematic for the "good genes" explanation of attractiveness. It should be noted, however, that the "good genes" explanation makes a claim concerning how mate selection, at a point in human history prior to the introduction of modern medicine, has shaped psychological adaptations that mediate current mate preferences. Consequently, associations between actual health in modern humans and either facial attractiveness or facial symmetry are not necessarily predicted by a "good genes" explanation of the attractiveness–symmetry relationship. Thus, the perceptual analysis of symmetry may, in the evolutionary past, have benefited individuals by encouraging selection of healthy mates with consequent direct and indirect benefits for reproduction.

References

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Benson, P. J., & Perrett, D. I. (1991). Synthesising continuous-tone caricatures. *Image Vision Computing*, *9*, 123–129.

Bohrnstedt, G. W. (1970). Reliability and validity assessment in attitude measurement. In: G. F. Summers (Ed.), *Attitude measurement* (pp. 80–99). Chicago: Rand McNally and Company.

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer.

Enquist, M., & Arak, A. (1998). In: R. Dukas (Ed.), *Cognitive ecology* (pp. 21–87). Chicago: Chicago University Press.

Enquist, M., & Ghirlanda, S. (1998). Evolutionary biology—the secrets of faces. *Nature*, *394*, 826–827.

Evans, C. S., Wenderoth, P., & Cheng, K. (2000). Detection of bilateral symmetry in complex biological images. *Perception*, *29*, 31–42.

Feingold, A. (1992). Good-looking people are not what we think. *Psychological Bulletin*, *111*, 304–341.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*, 573–644.

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

Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of quality in men and women. *Evolution and Human Behavior*, *22*, 93–112.

Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science*, *9*, 8–13.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*, 390–423.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, Series B*, *268*, 39–44.

Mealy, L., Bridgestock, R., & Townsend, G. (1999). Symmetry and perceived facial attractiveness. *Journal of Personality and Social Psychology*, *76*, 151–158.

Miller, G. F., & Todd, P. M. (1998). Mate choice turns cognitive. *Trends in Cognitive Sciences*, *2*, 190–198.

Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, developmental stability and evolution*. Oxford: Oxford University Press.

Møller, A. P., & Thornhill, R. (1997). A meta-analysis of the heretability of developmental stability. *Journal of Evolutionary Biology*, *10*, 1–16.

Møller, A. P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: a meta-analysis. *American Naturalist*, *151*, 174–192.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S. E., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions, and male sexual attractiveness. *Proceedings of the Royal Society of London, Series B*, *268*, 1617–1623.

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behaviour*, *20*, 295–307.

Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgments of female attractiveness. *Nature*, *368*, 239–242.

Rhodes, G., Proffitt, F., Grady, J. M., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin and Review*, *5*, 659–669.

Rhodes, G., Sumich, A., & Byatt, G. (1999). Are average facial configurations attractive only because of their symmetry? *Psychological Science*, *10*, 52–58.

Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R., & Akamatsu, S. (2001). Attractiveness of facial averageness and symmetry in non-western cultures: in search of biologically based standards of beauty. *Perception*, *30*, 611–626.

Rhodes, G., Zebrowitz, L., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior*, *22*, 31–46.

Rowland, D. A., & Perrett, D. I. (1995). Manipulating facial appearance through shape and colour. *IEEE Computer Graphics and Applications*, *15*, 70–76.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness symmetry and cues to good genes. *Proceedings of the Royal Society of London, Series B*, *266*, 1913–1917.

Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and physical health. *Evolution and Human Behavior*, *20*, 71–76.

Swaddle, J. P., & Cuthill, I. C. (1995). Assymetry and human facial attractiveness—symmetry may not always be beautiful. *Proceedings of the Royal Society London, Series B*, *261*, 111–116.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: averageness, symmetry, and parasite resistance. *Human Nature*, *4*, 237–269.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–460.

Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews*, *72*, 497–548.