

Second to fourth digit ratio and face shape

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The average human male face differs from the average female face in size and shape of the jaws, cheekbones, lips, eyes and nose. It is possible that this dimorphism is determined by sex steroids such as testosterone (T) and oestrogen (E), and several studies on the perception of such characteristics have been based on this assumption, but those studies focussed mainly on the relationship of male faces with circulating hormone levels; the corresponding biology of the female face remains mainly speculative. This paper is concerned with the relative importance of prenatal T and E levels (assessed via the 2D : 4D finger length ratio, a proxy for the ratio of T/E) and sex in the determination of facial form as characterized by 64 landmark points on facial photographs of 106 Austrians of college age. We found that (i) prenatal sex steroid ratios (in terms of 2D : 4D) and actual chromosomal sex dimorphism operate differently on faces, (ii) 2D : 4D affects male and female face shape by similar patterns, but (iii) is three times more intense in men than in women. There was no evidence that these effects were confounded by allometry or facial asymmetry. Our results suggest that studies on the perception of facial characteristics need to consider differential effects of prenatal hormone exposure and actual chromosomal gender in order to understand how characteristics have come to be rated 'masculine' or 'feminine' and the consequences of these perceptions in terms of mate preferences.

Keywords: face shape; digit ratio; 2D : 4D; hormones; sexual dimorphism; geometric morphometrics

1. INTRODUCTION

In many species, including humans, testosterone (T) production and metabolism mobilize resources that encourage males to attract and compete for mates. Testosterone affects a number of facial features. In pubertal males, a high testosterone-to-oestrogen (T/E) ratio is thought to facilitate the lateral growth of the cheekbones, mandibles and chin, the forward growth of the bones of the eyebrow ridges and the lengthening of the lower face leading to a more robust face shape (Farkas 1981; Enlow 1996). The influence of oestrogen (E) leads to a more gracile facial shape with high eyebrows, less robust jaws and fuller lips.

Hormone markers are also present in females. The signalling value of many female body features is linked to age and its related E/T ratio. Johnston & Franklin (1993) have hypothesized that a female face rated attractive may be displaying hormone markers (high E/low T) that serve as reliable indicators of fecundity. Pubertal bone growth (brow ridges and lower jaw) is stimulated by androgens (Tanner 1978) and lip fullness parallels E-dependent fat deposits elsewhere on the female body (Farkas 1981).

Studies examining the perception of hormone markers in male and female faces have produced apparently incompatible results. For example, although a number of experimenters have demonstrated that some women favour a male face with a large jaw, and prominent brow ridges and cheek-bones (Grammer & Thornhill 1994; Scheib *et al.* 1999), other studies have reported that some British and Japanese females prefer a more female-looking male face with a shorter than average lower jaw (Perrett *et al.* 1998; Penton-Voak *et al.* 1999). Still others have found that a mixture of mature features (large lower jaw, prominent cheek-bones and thick eyebrows) and neotenous features (large eyes and small nose) is the configuration of male faces women rate most highly (Cunningham *et al.* 1990). Some of these inconsistencies across studies are thought to result from the different procedures used to generate the male facial stimuli (for further discussion see Penton-Voak & Chen 2004).

While facial characteristics in the articles cited were typically measured as single distances or ratios, there is much insight to be gained by treating this shape as a whole (which is, after all, how it is perceived by the viewer of the opposite sex). Methods for this kind of analysis have not yet been introduced into the study of human attractiveness, and it seemed appropriate to incorporate them into the investigation of these developmental endocrinological hypotheses as well. Geometrics morphometrics methodology (GMM) is a group of analytical methods for the multivariate statistical analysis of Cartesian coordinate data of landmark point locations. These methods preserve complete information about the relative spatial relationships of landmarks throughout an analysis and, by utilizing the properties of Kendall's shape space, allow for the visualization of group differences and individual variations.

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In the present study we make use of the GMM for the study of possible associations between human finger length patterns (2D: 4D) and variation in facial shapes of males and females. The 2D: 4D ratio shows a pattern of mean difference by sex that appears to be established at a very early age and is correlated with T concentrations (Manning et al. 1998; Ronalds et al. 2002). Many studies provide indirect evidence that T stimulates prenatal growth of the fourth finger while E promotes the growth of the second finger (see for review Manning 2002). A low 2D: 4D ratio (fourth finger longer than the second) may thus act as a marker for a uterine environment high in T and low in E, and such a ratio is more often seen in males. Conversely, a high 2D: 4D ratio may serve as a marker for a uterine environment low in T and high in E, more often found in females. A recent study also provided direct evidence for the association between 2D: 4D and prenatal sex steroids. Lutchmaya et al. (2004) obtained radioimmunoassays of foetal testosterone (FT) and foetal estradiol (FE) from routine amniocentesis. They measured 2D : 4D ratios at age 2 years and found a negative correlation with FT/FE ratio independent of sex.

As 2D : 4D is thought to be a pointer to the early hormonal environment (i.e. the T/E ratio), we expected a low 2D : 4D (as a result of high T) to correspond to a somewhat more robust ('male-like') facial shape, whereas high 2D : 4D (as a result of high E) could correspond to a more gracile ('female-like') facial shape. We further hypothesized that this holds true for both males and females in a similar way, so that effects of early exposure to sex steroids are different from the classic list of sexually dimorphic features. If this hypothesis were true, it would (i) lend support to the effects of prenatal androgens (as indicated by 2D : 4D ratio) on facial shape, and (ii) contribute to the debate over the causal relations between hormones and facial features and attributions regarding such characteristics.

2. MATERIAL AND METHODS

(a) Participants

Our sample comprised 106 volunteers from undergraduate courses at the University of Vienna (50 males and 56 females). The mean age of the sample was 22.8 years (range 18–38, s.d.=4.0). These participants were selected from an original sample of 260 volunteers after excluding all those who were not exclusively heterosexual (by self-report), who were not right-handed, or who had suffered from any kind of injuries to the fingers. Likewise, images not meeting the standardization criteria (explained below) were excluded. Participants were informed of the purpose of the present study and gave their informed written consent.

(b) Procedure

(i) Data recording

We measured the lengths of the second and fourth digits of the left and right hands from the tip of the finger to the ventral proximal crease from photocopies. Where there was a band of creases at the base of the digit, we measured from the most proximal of these. It is known that these measurements can be made with high repeatability from photocopies of the hand and that they correlate strongly with 2D : 4D calculated from total digit length measured from X-rays of the fingers (Manning *et al.* 2000). All measurements were made to 0.01 mm with digital vernier calipers (although the actual reference points cannot possibly be located to that precision).

Colour digital images of each participant's face were taken with a digital single-lens reflex camera at high resolution in TIFF file format under standardized light conditions (Hedler Studio Lights, Hedler GmbH) and in frontal view. Participants were advised to remove any facial adornment, to look directly into the camera (in place of a more osteological standardization, such as the Frankfort Horizontal) and to present a neutral facial expression. Images apparently failing to meet these criteria, such as images of persons smiling, were excluded from the analysis (for other exclusions see above). Camera distance was kept constant at 3 m; the slight optical distortions of true facial form entailed in this finite spacing are ignored in the analysis that follows.

(ii) Facial shape analysis

The shape of each face was defined by manually setting 64 predetermined feature points ('landmarks') on each image. While this represents no standard anthropometric scheme (indeed, there is no such point scheme for facial photographs), it seems to us to be reasonable and thorough; the nearest comparable somatometric method may be Knussmann's (1988). From these points, 32 could be unambiguously identified in every case at positions that could plausibly be claimed to correspond from face to face on biological or perceptual grounds. The remaining landmarks lie on curves (e.g. the outline of the jaw or the lips) that are homologous among individuals but along which no exact landmark positions can be identified in the direction along the curve (figure 1a). These points were thus treated as semi-landmarks (Bookstein 1997; Gunz et al. 2005). At a semi-landmark, only the coordinate perpendicular to the curve comes from the actual data; its position along the curve is estimated by the 'sliding landmark' algorithm so as to remove any information from the analysis that is an artifact of landmark spacing. Such semi-landmarks can be treated as homologous landmarks in the subsequent statistical analysis.

The 64 landmarks of the 106 faces-a total of 13 568 coordinates-were analysed using the geometric morphometric toolkit, which is based on the landmark coordinates themselves rather than on calculated or measured distances among the landmarks. The mathematical theory and biological application of geometric morphometrics are well understood (Bookstein 1991, 1996; Marcus et al. 1996; Dryden & Mardia 1998; O'Higgins 2000; Slice 2005), and its statistical properties have been proven superior to those of distance or angle-based methods (Rohlf 2000a,b, 2003). The first step in the geometric morphometric analysis is the so-called Procrustes superimposition of the raw landmark coordinates. All landmark configurations are translated to the same origin (centroid), scaled to the same size (centroid size (CS), which is the square root of the sum of the variances of the x-coordinate and the y-coordinate within each case) and rotated to minimize the variance of within-landmark position summed over all landmarks in the configuration (Rohlf & Slice 1990). The resulting Procrustes coordinates (figure 1b) capture shape information only and can be used for subsequent multivariate statistical analyses. One major advantage of geometric morphometrics is that statistical results like multivariate regressions and principal components emerge in terms of landmark coordinates and can thus be visualized as shapes or shape changes in the original space. In this paper we exploit the latter version, showing the effects of

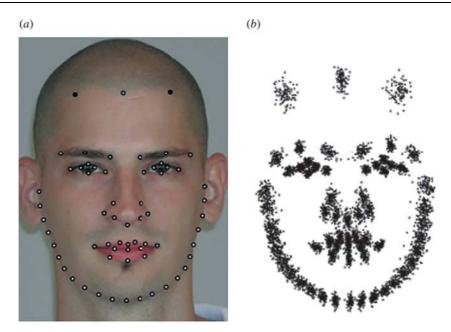


Figure 1. (a) An example face with 64 predefined landmarks. The grey-filled circles indicate classical landmarks that can be identified unambiguously, the white-filled circles are semi-landmarks that lie on a curve (see §2), and the forehead boss points (solid black) are used for visualization only and are not included in the statistical analyses. (b) All 106 landmark configurations superimposed by the Procrustes fit. These coordinates are the basis for further statistical analysis.

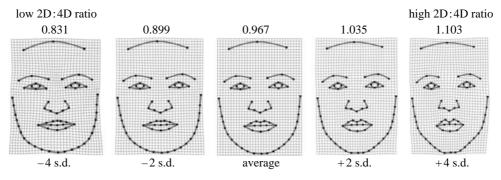


Figure 2. Visualization of the shape regression on 2D : 4D ratio (averaged among both hands) within males. The middle face with an undeformed square grid is the average landmark configuration and corresponds to the average digit ratio for males. The right grids show deformations from the mean face to faces that are predicted for higher 2D : 4D ratios (0.068=2 s.d. and 0.136=4 s.d., respectively, higher than the average). The left faces correspond to low 2D : 4D ratios (-2 s.d. and -4 s.d.). The ± 4 s.d. values are outside the data range.

a change both on the form and on a grid superimposed over the average form. The grid depicted, a *thin-plate spline* (TPS; Bookstein 1991), is the customary choice in this field, as its assumptions are consistent with those underlying the Procrustes method of superposition.

To assess the association between facial shape and 2D: 4Dratio we performed a regression of the full vector of Procrustes shape coordinates on the 2D: 4D ratio (one hand at a time). The alpha level of significance of this regression was calculated by a Monte Carlo permutation test (Good 2000) with the generalized shape variance explained by the regression (sum of the variances explained by 2D: 4D over all the shape coordinates separately) as the test statistic.

3. RESULTS

(a) Digit ratio

As found in previous studies (e.g. Manning *et al.* 1998; Manning 2002), males had a lower average 2D : 4D ratio than females both on the right hand and on the left hand and the mean differences were significant both with a parametric *t*-test (2D : 4D right hand: males 0.969 ± 0.036 , females 0.983 ± 0.034 , t = -2.16, p = .032, two-tailed; 2D : 4D left hand, males 0.965 ± 0.038 , females 0.985 ± 0.040 , t = -2.89, p = .004, two-tailed) and a non-parametric permutation test (right hand: p = .016, left hand: p = .003).

(b) Facial shape

Figure 2 shows the results of the shape regression on 2D : 4D ratio within males. The middle face with an undeformed square grid is the average landmark configuration. The right faces correspond to 2D : 4D ratios that are 0.068 (2 s.d.) and 0.136 (4 s.d.), respectively, higher than the average. The left faces correspond to low 2D : 4D ratios (-2 s.d. and -4 s.d.). The corresponding TPS deformation grids illustrates how the picture around the average shape has to be deformed to result in the target landmark configuration. For instance, it directly visualizes the compression of the lower jaw (especially the chin) relative to the midface that is presumed to be produced by the same features causing the higher 2D : 4D ratio. As this study is of shape only, all local size differences have to be seen as relative to other regions—total size remains the

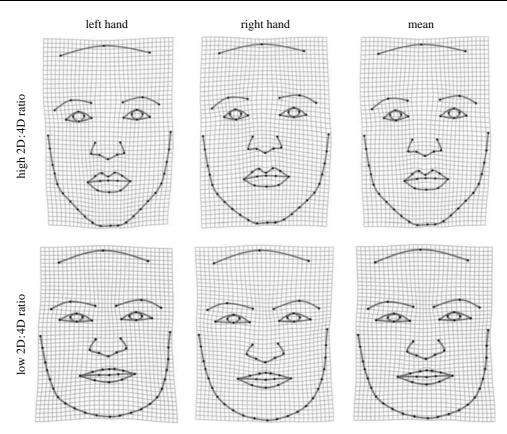


Figure 3. Shape regression within males on the 2D : 4D ratio of the left hand (upper and lower left figures), the right hand (middle figures), and the mean 2D : 4D ratio (right figures). The three upper figures are visualizations of predicted faces for 2D : 4D ratio 4 s.d. higher than the average. Accordingly, the lower figures are predicted faces for 2D : 4D ratio 4 s.d. lower than the average.

same in all faces. Conversely, the left faces in figure 2 correspond to a low 2D : 4D ratio. The main shape changes associated with the 2D : 4D ratios are the shape of the lips and the breadth of the jaws, the zygomatic arch, and the chin.

A Monte Carlo permutation test of the shape regression rejects the null hypothesis of no association between facial shape and 2D : 4D ratio with p < 0.05. When confining the analysis to the first five pairs of partial warps only (i.e. the 10 dimensions in shape space with the most large-scale shape deformations, see Bookstein 1991; Rohlf 1995), the regression is significant with p < 0.005. An additional validation for the stability of the result is the fact that the regressions for the left and for the right hand are very similar (figure 3).

Figure 4 visualizes the results of the shape regression on the 2D : 4D ratio for females. Although the deformation grids resemble those for males in figure 3, the regression for females is less stable and not significant. Moreover, the shape change predicted for an increase in 2D : 4D ratio is about three times higher in males than in females. The vector norms of the regression slope vectors are 0.197 and 0.069, respectively: these are in units of Procrustes distance per unit change in 2D : 4D.

Facial shape differs significantly between the sexes (permutation test, p < 0.001 after 3000 permutations). Figure 5 illustrates the actual mean difference of facial shape by sex as deformation grids. We did not find a relationship between 2D : 4D ratios and body height or CS offacial landmarks (for all four correlations of 2D : 4D with either CS or body height within both sexes $R^2 < 0.04$ and p > 0.2, *F*-test.). Correspondingly, the visualizations of

Proc. R. Soc. B (2005)

both 2D : 4D ratios and sexual dimorphism and associated facial shape did not change appreciably when corrected for body height or CS. Further, there was no significant relationship between 2D : 4D ratio and facial asymmetry calculated after Mardia *et al.* (2000) either when the analysis was based on all landmarks and semi-landmarks or when we used only the 30 most reliable landmarks: for all correlations between 2D : 4D ratio and asymmetry—using both fluctuating asymmetry and total asymmetry, within each sex separately and over both sexes, both landmark sets— $R^2 < 0.006$ and p > 0.5, *F*-test.

4. DISCUSSION

The aim of this study was to examine possible relationships between finger length ratios (2D : 4D) and facial shape of males and females. As reported in previous studies (e.g. Manning 2002), we also found a sex difference in 2D : 4D ratio with males, on the average, having lower 2D : 4D ratio than females on both hands.

Shape regression of the facial landmark coordinates upon 2D : 4D ratio for both male and female faces shows that some characteristics which are considered typically 'male' correspond to low 2D : 4D ratios, whereas some typically 'female' features correspond to high 2D : 4D ratios. To our knowledge, this is the first investigation regarding variation of facial shape that visualizes characteristics associated with high and low levels of prenatal sex steroids (as measured by proxy via 2D : 4D ratio). Moreover, these effects show a different pattern than the actual facial sexual dimorphism (as shown in figure 5) and we found no evidence that these effects were confounded

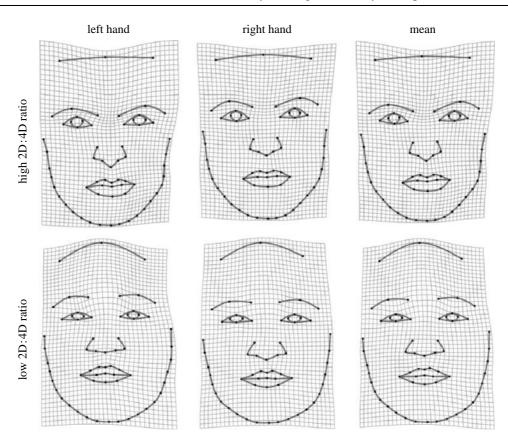


Figure 4. Shape regression within females on the 2D: 4D ratio of the left hand (left figures), the right hand (middle figures), and the mean 2D: 4D ratio (right figures). The three upper figures are visualizations of predicted faces for 2D: 4D ratio 6 s.d. higher than the average. Accordingly, the lower figures are predicted faces for 2D: 4D ratio 6 s.d. lower than the average.

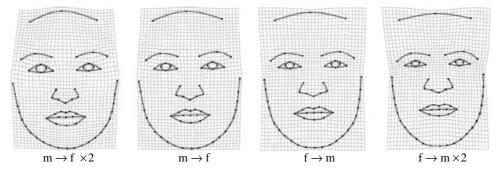


Figure 5. Sexual dimorphism in facial shape. The two inner deformation grids are thin-plate spline visualizations of the shape differences between the average male face (m) and the average female face (f). To enhance the details these differences were exaggerated by two in the outer grids.

by allometry or facial asymmetry. The fact that body height likewise was not significantly related to 2D : 4D or CS of facial landmarks supports this view and is in line with previous studies that also did not find a significant relationship between 2D : 4D with age or body height (Manning 2002; Lippa 2003).

According to Mazur & Booth (1998), early exposure to higher levels of T is likely to produce more male-like characteristics (masculinization) and fewer female characteristics (defeminization), whereas less exposure to T causes the reverse. These pre- and perinatal hormone effects are claimed to organize the architecture of the brain and body (e.g. McEwen 1988). In humans, there is, however, only limited evidence available for this claim, perhaps in part for ethical reasons (i.e. the assessment of foetal sex steroids is not warranted without a clinical indication and only longitudinal data would empirically support the claims here). Research on human facial characteristics, therefore, has concentrated on the correlates of physical features and actual levels of sex steroids. In particular, the link between hormones and human facial features is a much-discussed topic in human evolutionary biology.

Yet, there is little empirical evidence to support many of the theories put forward. In one recent study, Swaddle & Reierson (2002) noted that most of the previous studies on facial appearance had not considered actual measures of T. Swaddle & Reierson (2002) themselves used data from men with natural T levels and also from men with low levels of T (taken from Verdonck 1997; Verdonck *et al.* 1999) to manipulate facial characteristics (e.g. face height, lower jaw) accordingly in order to isolate the effects of T on facial shape. Females were asked to rate the dominance and attractiveness of these faces, and it was found that the

'high-T' faces produce higher dominance ratings but were not rated more attractive. Neave et al. (2003) found that low 2D : 4D ratios in males were significantly related to female perceptions of male dominance and masculinity but, again, not to attractiveness, consistent with the supposition by Swaddle & Reierson (2002) that features developed under the influence of testosterone do not directly account for attractiveness but rather for male dominance and masculinity. However, Neave et al. (2003) did not find substantial correlations between circulating levels of T and dominance, masculinity or attractiveness, leading them to speculate that any association between these features operates only at an early stage in life. More recently, Penton-Voak & Chen (2004) investigated the relationship between circulating levels of T and facial appearance. They constructed composites from faces of men with high and low T and had them rated for facial masculinity and attractiveness. 'High-T' composites were judged more masculine.

These studies suggest that human faces display the so-called--'hormone markers', honest cues to fertility and health that are known to affect judgments of facial characteristics (e.g. Fink & Penton-Voak 2002). Common to all such studies is the supposition that the signals which make a male typically 'male' and a female typically 'female' should be key signals for ratings of attractiveness in mate choice (for review see Grammer et al. 2003). However, although there is accumulating evidence from previous research for links between facial characteristics and sex steroids, it is still unknown how and at what stages of ontogeny they affect changes in facial shape. Furthermore, most studies have investigated associations between T and male facial characteristics, while data on the relationship between female facial characteristics and E remain speculative since they have been studied only at the perceptual level. For instance, some studies have found that women with a small mouth and full lips were rated attractive, because they are supposed to demonstrate high E levels and thus optimal fertility hormone profiles (Johnston & Franklin 1993; Thornhill & Gangestad 1999). Again, as for the studies on male facial appearance we cited earlier, these conclusions on female facial characteristics were drawn mainly without having information on actual hormone levels and remain mainly speculative since the relation between sex steroids and facial appearance was not quantified. Digit ratio has been suggested to be related to foetal growth and there is now direct and indirect evidence that 2D : 4D is established in utero and is negatively related to prenatal T and positively with prenatal E (Lutchmaya et al. 2004).

In view of the data we present here, facial characteristics that have been previously reported to be perceived as typically 'masculine' or 'feminine' may be a composite of at least two factors operating differently on facial shape. The first factor is the prenatal environment's levels of sex steroids. It may be that T *per se* rather than E or T/E ratio is the candidate, as the shape regressions on 2D : 4D ratios are very similarly patterned for men and women but much stronger for men. Actual chromosomal sex dimorphism must be regarded as a separate, second factor. It is visualized in the grids (figure 5) by the more pronounced lower male face, presumably reflecting its extended growth, whereas the prenatal hormonal environment affects another dimension which is supposedly 'robusticity'. As male faces, on average, show both hypermorphosis (Enlow 1996; Rosas & Bastir 2002; Schaefer *et al.* 2004; Bulygina *et al.* in press) and score higher on robusticity than females (due to lower 2D : 4D ratios), it is likely that the composite of both of these characteristics together is perceived (and found in rating studies) as 'masculine'. We suggest that future studies on facial characteristics and the perception of them need to consider these differential effects on facial shape in order to get a more accurate picture of what causal association between hormones and facial features is actually perceived and rated when viewing facial stimuli.

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REFERENCES

- Bookstein, F. 1991 Morphometric tools for landmark data: geometry and biology. New York: Cambridge University Press.
- Bookstein, F. 1996 Biometrics, biomathematics and the morphometric synthesis. *Bull. Math. Biol.* 58, 313–365. (doi:10.1016/0092-8240(95)00329-0.)
- Bookstein, F. 1997 Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Med. Image Anal.* **1**, 225–243. (doi:10.1016/S1361-8415(97)85012-8.)
- Bulygina, E., Mitteroecker, P. & Aiello, L. C. in press Ontogeny of facial dimorphism and patterns of individual development within one human population, *Am. J. Phys. Anthropol.*
- Cunningham, M. R., Barbee, A. P. & Pike, C. L. 1990 What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *J. Pers. Soc. Psychol.* 59, 61–72. (doi:10. 1037//0022-3514.59.1.61.)
- Dryden, I. L. & Mardia, K. V. 1998 Statistical shape analysis. New York: Wiley.
- Enlow, D. H. 1996 *Essential of facial growth*. Philadelphia: W.B. Saunders Company.
- Farkas, L. G. 1981 Anthropometry or the head and face in Medicine. New York: Elsevier.
- Fink, B. & Penton-Voak, I. S. 2002 Evolutionary psychology of facial attractiveness. *Curr. Dir. Psychol. Sci.* 11, 154–158. (doi:10.1111/1467-8721.00190.)
- Good, P. 2000 Permutation tests: a practical guide to resampling methods for testing hypotheses. New York: Springer.
- Grammer, K. & Thornhill, R. 1994 Human facial attractiveness and sexual selection: the roles of averageness and symmetry. J. Comp. Psychol. 108, 233–242. (doi:10.1037// 0735-7036.108.3.233.)
- Grammer, K., Fink, B., Møller, A. P. & Thornhill, R. 2003 Darwinian aesthetics: sexual selection and the biology of beauty. *Biol. Rev.* **78**, 385–407. (doi:10.1017/S146479310 2006085.)
- Gunz, P., Mitteroecker, P. & Bookstein, F. 2005 Semilandmarks in three dimensions. In *Modern morphometrics in physical anthropology* (ed. D. E. Slice). Dodretch: Kluwer Academic.
- Johnston, V. S. & Franklin, M. 1993 Is beauty in the eye of the beholder? *Ethol. Sociobiol.* 14, 183–199. (doi:10.1016/ 0162-3095(93)90005-3.)
- Knussmann, R. 1988 Somatometrie. In Handbuch der vergleichenden Biologie des Menschen. Band I. Teil. 1 (ed. R. Knussmann), pp. 232–285. Stuttgart: Fischer.

- Lippa, R. A. 2003 Are 2D : 4D finger-length ratios related to sexual orientation? Yes for men, no for women. J. Pers. Soc. Psychol. 85, 179–188. (doi:10.1037/0022-3514.85.1.179.)
- Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R. & Manning, J. T. 2004 Second to fourth digit ratios, fetal testosterone and estradiol. *Early Hum. Dev.* 77, 23–28. (doi:10.1016/j.earlhumdev.2003.12.002.)
- Manning, J. T. 2002 *Digit Ratio: a pointer to fertility, behaviour, and health.* New Brunswick: Rutgers University Press.
- Manning, J. T., Scutt, D., Wilson, J. & Lewis-Jones, D. I. 1998 The ratio of second to fourth digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Hum. Reprod.* 13, 3000–3004. (doi:10.1093/humrep/13.11.3000.)
- Manning, J. T., Trivers, R. L., Thornhill, R. & Singh, D. 2000 The 2nd : 4th digit ratio and asymmetry of hand performance in Jamaican children. *Laterality* 5, 121–132. (doi:10.1080/135765000396744.)
- Marcus, L. F., Corti, M., Loy, A., Naylor, G. & Slice, D. E. (eds) 1996 *Advances in morphometrics*. New York: Plenum Press.
- Mardia, K. V., Bookstein, F. L. & Moreton, I. J. 2000 Statistical assessment of bilateral symmetry of shapes. *Biometrika* 87, 285–300. (doi:10.1093/biomet/87.2.285.)
- Mazur, A. & Booth, A. 1998 Testosterone and dominance in men. *Behav. Brain Sci.* 21, 353–397. (doi:10.1017/ S0140525X98001228.)
- McEwen, B. S. 1988 Actions of sex hormones on the brain: 'organization' and 'activation' in relation to functional teratology. *Prog. Brain Res.* **73**, 121–134.
- Neave, N., Laing, S., Fink, B. & Manning, J. T. 2003 Second to fourth digit ratio, testosterone, and perceived male dominance. *Proc. R. Soc. B* 270, 2167–2172. (doi:10. 1098/rspb.2003.2502.)
- O'Higgins, P. 2000 The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. *J. Anat.* **197**, 103–120. (doi:10.1046/j.1469-7580.2000.19710103.x.)
- Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Appl. Opt.* **394**, 884–887. (doi:10.1038/ 29772.)
- Penton-Voak, I. S. & Chen, J. Y. 2004 High salivary testosterone is linked to masculine male facial appearance in humans. *Evol. Hum. Behav.* **25**, 229–241. (doi:10.1016/j.evolhumbehav.2004.04.003.)
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Female preference for male faces changes cyclically. *Appl. Opt.* **399**, 741–742. (doi:10.1038/21557.)

- Rohlf, F. J. 1995 Statistical analysis of shape using partialwarp scores. In *Proc. Curr. Issues Stat. Shape Anal.* (ed. K. V. Mardia & C. A. Gill), pp. 154–158. Leeds University Press.
- Rohlf, F. J. 2000a On the use of shape spaces to compare morphometric methods. *Hystrix*, *Italian J. Mammol.* 11, 9–25.
- Rohlf, F. J. 2000b Statistical power comparisons among alternative morphometric methods. Am. J. Phys. Anthropol. 111, 463–478. (doi:10.1002/(SICI)1096-8644(200004) 111:4<463::AID-AJPA3>3.0.CO;2-B.)
- Rohlf, F. J. 2003 Bias and error in estimates of mean shape in geometric morphometrics. *J. Hum. Evol.* 44, 665–683. (doi:10.1016/S0047-2484(03)00047-2.)
- Rohlf, F. J. & Slice, D. E. 1990 Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zool.* **39**, 40–59.
- Ronalds, G., Phillips, D. I., Godfrey, K. M. & Manning, J. T. 2002 The ratio of second to fourth digit lengths: a marker of impaired fetal growth? *Early Hum. Dev.* 68, 21–26. (doi:10.1016/S0378-3782(02)00009-9.)
- Rosas, A. & Bastir, M. 2002 Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. Am. J. Phys. Anthropol. 117, 236–245. (doi:10.1002/ajpa.10023.)
- Schaefer, K., Mitteroecker, P., Gunz, P., Bernhard, M. & Bookstein, F. L. 2004 Craniofacial sexual dimorphism patterns and allometry among extant hominoids. *Ann. Anat.* 186, 471–478.
- Scheib, J., Gangestad, S. W. & Thornhill, R. 1999 Facial attractiveness, symmetry and cues of good genes. *Proc. R. Soc. B* 266, 1913–1917. (doi:10.1098/rspb.1999.0866.)
- Slice, D. E. 2005 Modern morphometrics in physical anthropology. Dodretch: Kluwer Academic.
- Swaddle, J. P. & Reierson, G. W. 2002 Testosterone increases perceived dominance but not attractiveness in human males. *Proc. R. Soc. B* 269, 2285–2289. (doi:10.1098/rspb. 2002.2165.)
- Tanner, J. M. 1978 Foetus into man: physical growth from conception to maturity. London: Open Books.
- Thornhill, R. & Gangestad, S. W. 1999 Facial attractiveness. *Trends Cogn. Sci.* **3**, 452–460. (doi:10.1016/S1364-6613 (99)01403-5.)
- Verdonck, A. 1997 Effect of testosterone on craniofacial growth in the human and the rat. Leuven: Katholieke Universiteit te Leuven.
- Verdonck, A., Gaethofs, M., Carels, C. & de Zegher, F. 1999 Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. *Eur. J. Orthod.* 21, 137–143. (doi:10.1093/ejo/21.2.137.)

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