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Female appearance: facial and bodily attractiveness as shape

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Abstract

Human physical attractiveness is supposed to reflect developmental stability (i.e. the ability of individuals to maintain stable development of their morphology under a given environmental condition) and physiological status. Hence, evolutionary psychologists have suggested that appearance may not only reveal so called 'honest signals' but even comprise a single ornament of mate value. However, it is still a matter of debate which physical features affect the ratings of female beauty, and whether these features are truly associated with aspects of developmental and physiological status. Here we present morphometric data of images of faces and bodies from 92 women together with ratings of attractiveness by 60 men. A total of 101 somatometric landmarks were digitized as two-dimensional coordinates from three views: facial, front and back full-body view. These image sets were analyzed separately by means of geometric morphometric methodology (GMM). Attractiveness ratings of the face and body were significantly associated with both (i) the amount of fluctuating asymmetry (as a measure of developmental stability), and (ii) specific localized shape differences in regions of known estrogen sensitivity. The results support the notion that ratings of women's physical attractiveness are indeed based on indicators of developmental stability and physiological status.

Key words: evolutionary psychology, face shape, physical attractiveness, fluctuating asymmetry, hormone markers, geometric morphometrics

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Human beauty standards seem to reflect our evolutionary distant and recent past and emphasize the role of health assessment in mate choice. Evolutionary psychologists have addressed the question of what beauty really means by analyzing the attractiveness of visual characters of the face and the body in three main contexts: the impact of symmetry, averageness, and sexually dimorphic features ('hormone-markers') (for a review, see: Grammer *et al.,* 2003).

Symmetry

Symmetry of bilaterally represented traits is positively correlated with heterozygosity in many animals, including humans (see Thornhill & Gangestad, 1999 for a review) and is thought to display resistance against parasites and pathogens (Thornhill & Gangestad, 1993). If that be true, bilateral symmetry of the face and body reflects overall quality of development, especially the ability to resist environmental perturbations during early development, which implies that symmetry of physical characteristics indicates developmental homeostasis (Thornhill & Gangestad, 1993). It is well established that poor environmental conditions increase developmental instability resulting in higher values of fluctuating asymmetry (FA), i.e. random deviations from bilateral symmetry in a morphological character (van Valen, 1962; Thornhill & Møller, 1997). Furthermore, symmetry of secondary sexual characteristics of the face is thought to display immunocompetence because it is expected to require higher titers of sex hormones in order to construct symmetrical – especially large – secondary sexual traits (Thornhill & Gangestad, 1993; 1999).

Many studies demonstrate the direct effects of symmetry on attractiveness (Grammer & Thornhill, 1994; Little & Jones, 2003), while other research suggests that symmetry can be associated with attractiveness for reasons other than direct effects of symmetry *per se* (Scheib *et al.,* 1999). Enquist and Arak (1994) and also Johnstone (1994) offered an alternative account, arguing that symmetry is more readily perceived by the visual system. In this view, the preference for symmetry is thought to be merely a by-product of the design of the perceptual system rather than an adaptation.

Averageness

Thornhill and Gangestad (1993) investigated the link between symmetry and averageness and suggested that preference for average traits could have evolved because in continuously heritable traits the average denotes genetic heterozygosity. Heterozygosity could signal an outbred mate or provide genetic diversity in defense against parasites and pathogens. In fact, studies indicate that average faces are attractive (Langlois & Roggmann, 1990) but can be improved upon by some specific non-average features (Alley & Cunningham, 1991). A study by Halberstadt and Rhodes (2000) reports that averageness and attractiveness correlate for non-face averages. It may therefore be that humans have a general proclivity towards prototypical exemplars, and that their attraction to average faces is a reflection of this more general attraction. As for symmetry, the contribution of averageness to attractiveness is still debated (Thornhill & Gangestad, 1999). Exactly what features contribute to the averageness effect remains speculative.

Hormone markers

In many species, including humans, sex steroid production and metabolism mobilize resources for the effort to attract and compete for mates (Ellison, 1998). Testosterone (T) and Estrogen (E) affect a number of facial and bodily features. In the human face the basic proportions are sexually dimorphic; male traits develop under the influence of T and female traits develop under the influence of E. For example, in pubertal males, facilitated by a high T/E ratio, the cheekbones, mandibles and chin grow laterally, the bones of the eyebrow ridges grow forward, and the lower facial bone lengthens (Farkas, 1981; Symons, 1995). In females, the signaling value of many body features is linked to age and reproductive condition, both of which correspond to a woman's E/T ratio (Symons, 1995; Thornhill & Grammer, 1999), attractive signals corresponding to high ratios. E promotes women's fertility, but it could be a handicap sex hormone for women similar to how T acts for men (Service, 1998; Dabbs, 2000). Morphological markers of high E may reliably signal a female immune system of such high quality that it can deal with the potential toxic effects of very high E levels (Thornhill & Møller, 1997; Thornhill & Grammer, 1999).

The face and body as one ornament

That physical characteristics of women's faces and bodies are condition-dependent is corroborated by E facilitating the development of the adult female face, waist, hips, and thighs during the same period of ontogeny. The influence of E in shaping the adult female fat deposits in buttocks and thighs, breasts and lips is well established (Johnston & Franklin, 1993; Symons, 1995; Pond, 1998; Grammer *et al.*, 2003). Furthermore, E apparently facilitates the maturation of the facial bones, which affects lower face length and jaw size in women. A more recent study by Koehler and colleagues (2004) examined the relation of facial asymmetry and measures of facial masculinity and femininity and also facial sexual dimorphism and body asymmetry. These authors found no significant correlations between facial masculinity and any measures of asymmetry or ratings of symmetry in males; whereas in females facial femininity was indeed associated with body symmetry. Koehler *et al.* (2004) concluded that specifically for females, facial femininity and body symmetry may reflect similar aspects of mate quality.

This result is in accord with a previous study by Thornhill and Grammer (1999), who showed that independent attractiveness ratings in Austria and the U.S. of the same women in each of three poses (face, front nude with faces covered, and back nude) were significantly positively correlated. These authors consequently suggested that the human face and body together comprise one single condition-dependent ornament of mate value. Grammer and colleagues (2001) extended this approach and called it the 'n-dimensional feature space'. In this view, faces and bodies are considered a single whole, and the authors suggest that this reflects the mechanism by which the brain decides about attractiveness. The underlying idea is that physical traits evolved to honestly indicate an individual's condition (because selection for mate choosers, who use true fitness indicators in mate choice, would otherwise generate selection for competitive displayers that signal dishonesty). In other words: mate choosers are expected to pay attention primarily to physical traits that honestly or non-deviously advertise mate value (Gangestad, 2001; Gangestad & Simspon, 2000; Grammer *et al*., 2003).

Following this argument, the present paper stresses the questions of what physical features drive male assessments of female attractiveness, and whether these features are associated with aspects of women's developmental and hormonal status. Our approach differs from previous ones that mainly investigated the contributions to perceptions of female faces and bodies. The present study investigated the naturally occurring shape variation *predicted* by such ratings. In particular, we hypothesize that perceived attractiveness of female face and body (i) predicts shape changes in E-sensitive regions precisely the way E-levels are known to operate, and (ii) correlates negatively with FA levels in all three body views. If these hypotheses were solid, they would lend further support to the notion that the perception of women's physical appearance is based on morphological indicators of developmental and physiological status.

Material and methods

Stimulus material

Our material was the data set of photographs of 92 nude American women from the ages of 18 to 30 previously used by Thornhill and Grammer (1999) and Grammer and colleagues (2001). These women responded to an advertisement in the *Los Angeles Times* by the Japanese artist Akira Gomi. Gomi took photographs from three different views: face only and front and back views (from head to knee) separately of the body. Facial photographs were taken with neutral expression and were standardized for size, distance to the camera, and lighting. Gomi recorded subjects' age by self-report, together with measurements of body mass, height, and waist and hip circumference. Body mass index (BMI) as a commonly used measure of body fat was calculated as mass (in kilograms) divided by height squared (in meters squared; Kim *et al.*, 2004).

The three different pictures of each subject (with heads and hair masked for the front and back views) have been independently rated for attractiveness on a 1–7 Likert scale (where 7 is most attractive) by 60 American and Austrian men who self-reported their age (mean age 25 years, range 19–55 years) and ethnicity. Participants rated only one of the three sets, i.e., one view of all the women. Each set was rated by 10 men in each country; thus, there were 30 raters from Austria and 30 raters from the U.S. As Thornhill and Grammer (1999) found the mean attractiveness ratings between the Austrian and U.S. men to correlate highly for all three views, we continue here with the results for Austrian and American raters combined: the picture rated least attractive in the facial view scores at 1.4 whereas the most attractive one scores at 6.2 (mean value: 3.94 ±0.80). For the front view pictures, the arithmetic mean is 3.77 ±0.85 (ranging between 1.7 for the least attractively rated picture and 5.8 for the most attractive). Likewise, the mean rating for all back view images is 3.64 ±1.12 with the least and most attractive picture scoring at 1.6 and 6.5, respectively (for details see Thornhill & Grammer 1999).

Statistical analysis

Methodological prerequisites

The two dimensional (2D) coordinates of 101 somatometric landmarks (47 on the face, 32 on the front and 22 on the back view) were digitized from the photographs. They represent the maximum number of craniometric measurement points in two dimensions that meet the standards of reliable identifiability and geometric homology. Definitions of landmarks locations were mainly adjusted following Knussmann (1988). The digitized landmarks of the 92 faces – a total of 18584 coordinates – were analyzed for the three image sets separately by means of the geometric morphometric (GMM) toolkit, which is based on the landmark coordinates themselves rather than on calculated or measured distances between the landmarks. The mathematical theory and biological application of GMM are meanwhile well understood (Bookstein, 1991, 1996; Marcus *et al*., 1996; Dryden & Mardia 1998; Slice, 2005), and the statistical properties have been proven superior to those of distance or angle-based methods (Rohlf, 2000a, 2000b, 2003). The first step in the GMM analysis is the so-called *Procrustes superimposition* of the raw landmark coordinates. All landmark configurations are translated to the same origin (namely, the centroid), scaled to the same size (centroid size), and rotated to minimize the variance of within-landmark position summed over all landmarks in the configuration (Rohlf & Slice, 1990). The resulting Procrustes coordinates capture shape information only and can be used for subsequent multivariate statistical analyses.

One major advantage of GMM is that statistical results such as multivariate regressions emerge in terms of landmark coordinates and can thus be visualized. In this paper we show the effects of a shape change using the *thin-plate spline* (TPS, Bookstein, 1991) interpolation methodology. TPS deformation grids illustrate displacements of positions of landmarks by modeling the deformations taking place between the landmarks, i.e. in all regions without landmark points. Grid depiction is the customary choice in this field, as its assumptions are consistent with those underlying the Procrustes superimposition method.

Asymmetry analysis

The standard approach to asymmetry in anthropology is based in terms of separate measures on the left and right sides of organisms (Ludwig, 1932). The total asymmetry (TA) of a bilateral object is a formal sum of directional asymmetry (DA) and fluctuating asymmetry (FA). The latter, as a measure of individual developmental stability, refers to a pattern of bilateral variation where variation on the right and left sides is both *random* and *independent*. In the case of DA ('laterality'), one side is consistently different from the other in conformation or size. DA implies (though does not demonstrate the presence of) repeatable effects of environment or genotype on asymmetry and thus conventionally does not qualify for use as a measure of developmental precision. It is usually assessed by the fact that the mean signed differences between the left and the right side deviate significantly from zero. If this is found in any trait under consideration, this trait is often excluded from the FA assessment. As our Procrustes superimposition approach shares with other GMM tools the general strategy of characterizing the landmark configuration as a geometric whole, it does not consider the size of the traits, but rather analyzes the geometric variation itself. Such classic methods are the topic of a considerable biometric literature (see Palmer & Strobeck, 2003), and their language of fluctuating and directional components of asymmetry of single measures applies directly without any biotheoretical adjustment to this quite different algebra (Schaefer *et al.*, 2006).

Procrustes symmetry analysis (Mardia *et al.*, 2000) was applied in order to quantify and *decompose* DA and FA from TA found in the complete landmark configuration under consideration by interchanging pairs of landmarks and comparing the original configurations and their relabeled reflections. The total sum of squares for squared shape distance between the original configurations and their relabeled reflections expresses what is conventionally identified with total asymmetry. The sum of squares for mean asymmetry, the squared shape distance between these two group means (original and mirrored data), corresponds to directional asymmetry. The within-cases sum of squares about this average, which expresses the extent to which the sample fluctuates about its own mean asymmetry, corresponds to fluctuating asymmetry. In this way, our analyses were based on multiple traits, thus providing higher accuracy for detecting stress (Leung *et al*., 2000) and circumventing the confounding of DA with FA that usually hinders clarification in these studies.

The main procedural steps in this method are as follows: (1) For each single form, a mirrored and appropriately relabeled form is produced. (2) The original forms, together with their mirrored counterparts, are projected into shape space using a general least square (GLS) Procrustes superimposition (Rohlf & Slice, 1990; Bookstein, 1998; Dryden & Mardia, 1998). (3) The vector of shape difference between each shape and its relabeled reflection is a measure of TA. The sample average of these vectors is an estimate of the DA. The deviation of these asymmetry vectors from their average is a measure of FA. (4) The total sum of squares of the individual vector differences is decomposed into two components, one for DA and the other for FA (Mardia *et al*., 2000).

Shape regressions

In order to determine the shape variation associated with attractiveness ratings a linear regression function was calculated for every shape coordinate separately, whereby the slopes of the functions predict the shape change that occurs within one unit of that independent variable. Shape regressions were visualized as TPS deformation grids by computing the mean form (consensus form) and adding the respective slopes to the corresponding shape coordinate. Since the changes within one unit are often small, the slopes are usually exaggerated by an arbitrary factor in order to improve their visibility (these factors can differ for the visualizations). The significance of these multivariate regressions was calculated using a Monte Carlo permutation test (Good, 2000) with the generalized shape variance explained by the regression (sum of the variances explained by attractiveness over all the shape coordinates separately) as the test statistic. All computations were done in MATHEMATICA 5.0 (Wolfram Research, Inc.).

In the subsequent sections, we consistently use the following abbreviations introduced above: GMM (geometric morphometric methods), DA (directional asymmetry), FA (fluctuating asymmetry), TA (total asymmetry), TPS (thin-plate-spline), E (estrogen), T (testosterone), BMI (body mass index) and WHR (waist-to-hip ratio).

Results

In this section, we begin by presenting the actual consensus configurations for the three body regions after the application of Procrustes superimposition (Fig. 1). This single set of landmarks represents the observed average configuration of the full sample. We then introduce the DA pattern for all three views. Its complexity demonstrates that these arrangements could not have been identified accurately with conventional mean signed magnitudes deviating significantly from zero (designed to detect differences in size). Then we study the relationship between the remaining FA level and the perceived attractiveness. The last part deals with the determination of how shape variation is predicted by the attractiveness ratings in all three views.

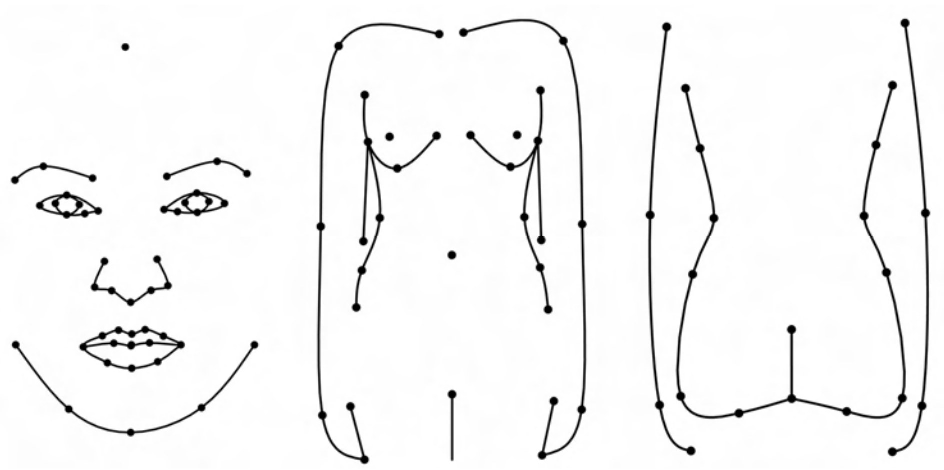

Figure 1:
Visualization of the average landmark configurations (consensus configuration) in the three views for the 92 women: face with landmarks in all main regions (the single dot at the top is *trichion*, the midpoint of the hairline) except cheekbones and corners of forehead, which were hidden by hair in several women (left); front view with black dot in the middle being the navel, surrounded by points for waist, upper pelvis and hip, and further landmarks at vulva, arms, hands, and breasts (middle); back view with landmarks for back, buttock and arms (right). All landmarks are indicated as black dots; connecting lines are drawn for visualization purposes.

Asymmetry and rated attractiveness

Face

Procrustes symmetry decomposition of the facial landmarks revealed a significant effect of DA ($p < 0.001$; F-test) for the 92 configurations which accounted for about 20% of TA (Figure 2). The TPS deformation grid shows that DA is manifested in a bending of the midline indicating a larger left lower face. For FA, there is a significant negative correlation with attractiveness ($r = -0.40$, $p < 0.01$; Permutation test). Clearly, highly asymmetric faces were rated less attractive on average.

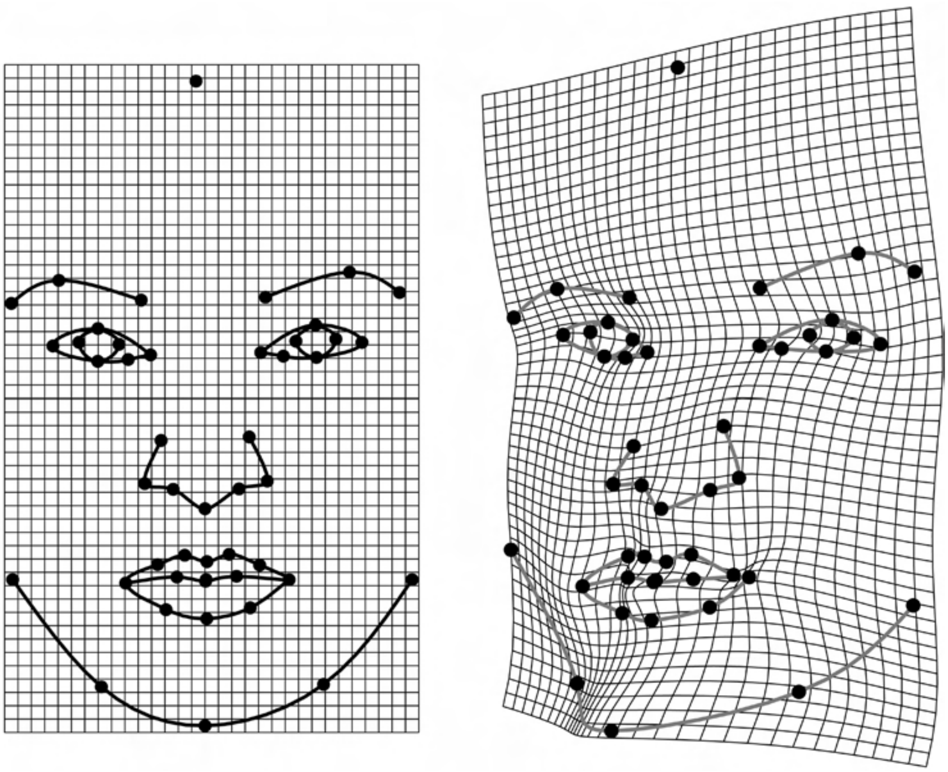

Figure 2:
Visualization of facial directional asymmetry by TPS deformation grids. The panels show the grand mean of the original configurations and their relabeled reflections ($n = 184$) with an undeformed square grid (left), and the DA for the sample of the 92 faces as shape change between the group means of the originals and their reflections. The grid indicates the specific landmark shifts magnified five times (right) for better readability.

Body

Likewise, the same analysis was applied to the landmarks of the body images. There was a significant effect of DA ($p < 0.001$; F-test) for the body landmarks in frontal view which explained about 21% of TA (Figure 3). We found a negative correlation of FA with attractiveness. Although the correlation coefficient at $r = -0.30$ is smaller than for the face, it is significant ($p < 0.05$; Permutation test).

The left panel in Figure 3 shows the grand mean of the original configurations of all 92 women and their reflections, while the TPS deformation grid for DA on the right indicates a compensation of the upper body – possibly due to a shorter average left leg.

In the back view (Figure 4) DA was found to be highly significant as well ($p < 0.001$; F-test); the TPS on the right shows the same upper body compensation as in front views. No significant correlation between FA and attractiveness ratings was found, though the observed coefficient was in the predicted direction: photos with higher fluctuating asymmetry of body parts received less attractive ratings on average.

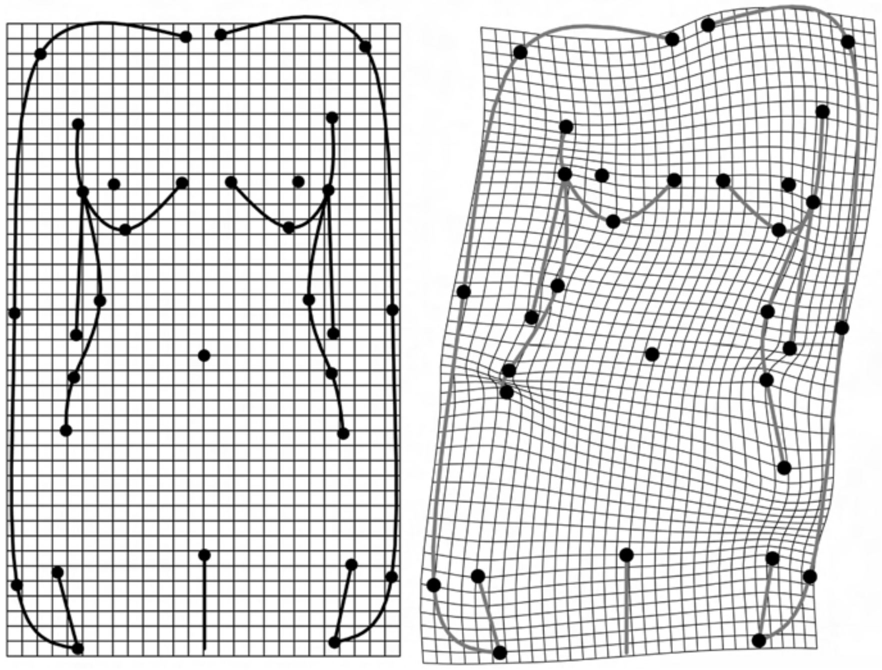

Figure 3:
Visualization of frontal directional asymmetry by TPS deformation grids. The panels show the grand mean of the original configurations and their relabeled reflections ($n = 184$) with an undeformed square grid (left), and the DA depicted for the 92 front views as shape change between the group means of the originals and their reflections. The grid indicates the specific landmark shifts magnified five times (right) for better readability.

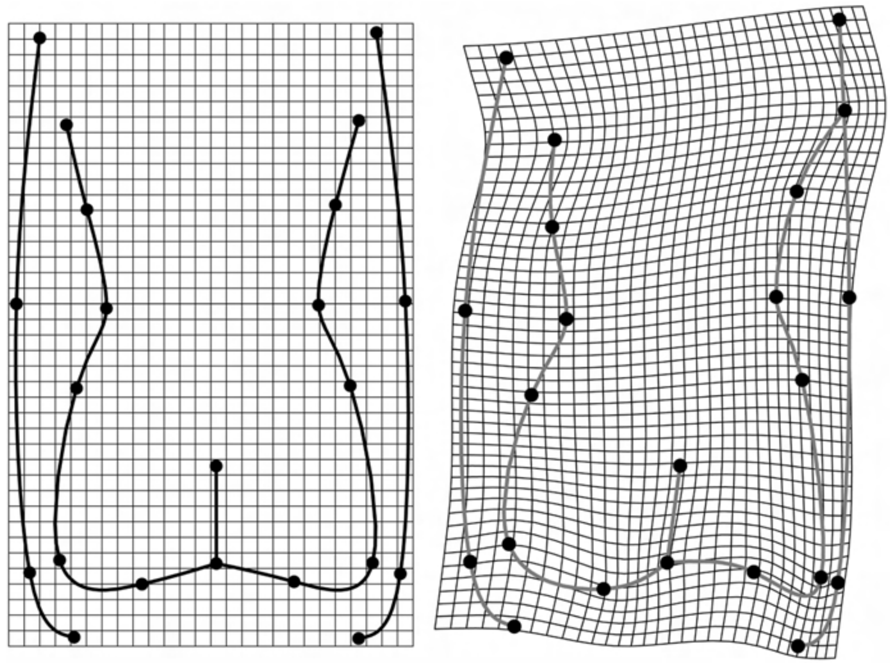

Figure 4:
Visualization of back view directional asymmetry by TPS deformation grids. The panels show the grand mean of the original configurations and their relabeled reflections (n = 184) with an undeformed square grid (left), and the DA found in the 92 back views as shape change between the group means of the originals and their reflections. The grid indicates the specific landmark shifts magnified five times (right) for better readability.

Shape predictions by perceived attractiveness

For the analysis of shape regressions upon attractiveness, we first considered the face.

Figure 5 (left) shows the TPS grid deformation that corresponds to *decreasing* attractiveness: the spline generally stretches, resulting in a longer face, a bigger nose, a more prominent chin and smaller lips. The opposite is true for the image on the right that visualizes the shape changes associated with *increasing* attractiveness. As indicated by the grid compression, the whole shape configuration appears rounder and the local deformations point to a more gracile nose and chin, and larger lips. A Monte Carlo permutation test of the shape regression rejects the null hypothesis of no association between facial shape and perceived attractiveness with $p < 0.01$.

The shape regressions upon rated attractiveness for the front and for the back views are shown in Figure 6 as predicted transformations in both directions from the consensus. There is a more horizontal grid compression in the deformations that accord with decreasing perceived attractiveness as opposed to a more vertical stretching. In front view, the regions

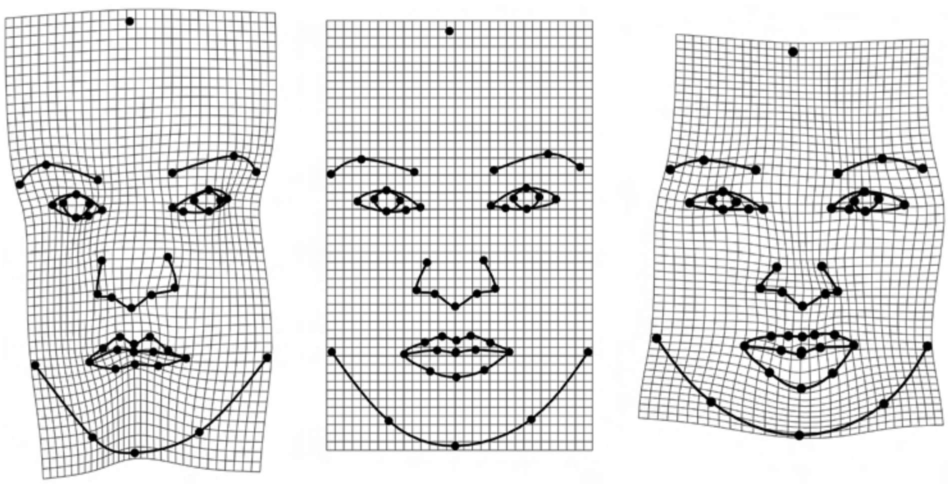

Figure 5:
Visualization of the shape regression on perceived female facial attractiveness by TPS deformation grids. The middle panel is the average landmark configuration (consensus) with an undeformed square grid, neighboring panels show the predicted transformation in both directions from this consensus: the deformation corresponds to a decrease (left) and increase (right), respectively, in ten units of the attractiveness scale. (The factor of ten here is chosen for optimal readability of the warp; the actual sample variation of about ± 2 units is too small for depicting the distortion appropriately).

where the grid bands most are the breasts and the abdomen. In shapes visualizing decreasing attractiveness, the grid around the breasts is stretched inferiorly whereas around the abdomen it is compressed. This expresses a relative enlargement of the waist diameter and greatest width of both pelvis and hip shifting upwards. Conversely, for increasing attractiveness, the shapes show a narrower waist and are rather stretched in the abdominal region. The higher position of the breasts is also evident. These shape regressions are significant at $p < 0.05$.

In order to study these interrelations independently of possible confounding effects of differences in women's body mass, we (geometrically) adjusted the shape regressions for BMI (Figure 7). From the three original vectors of regression slopes visualized in Figures 5 and 6, we projected out the corresponding regression vectors for shape on BMI (Burnaby, 1966; Mitteroecker *et al*., 2004). The corresponding regression vector for attractiveness is then perpendicular to the regression vector for BMI.

Each pair of grids represents both directions of deformation for the region involved. The adjustment for BMI did not change the deformation grids of the face (see Figure 2). Apart from the apparent localized grid deformation in the region of the breast – now combining the uplifting of the grid with its expansion for the shapes that accords with increasing rated attractiveness – the adjustment for BMI also effects major landmark rearrangements in the lower body region. For grids representing the transformation in the direction of decreasing perceived attractiveness, waist, hip, and upper pelvis landmarks are all laterally displaced and almost vertically aligned. In contrast, high attractive ratings predict landmark relationships in this region that indicate a comparably narrower waist along with a wider hip diameter. This situation is also evident in the back views: For the shape associated with high attractiveness ratings, the grid is stretched for the buttock landmarks but is vertically com-

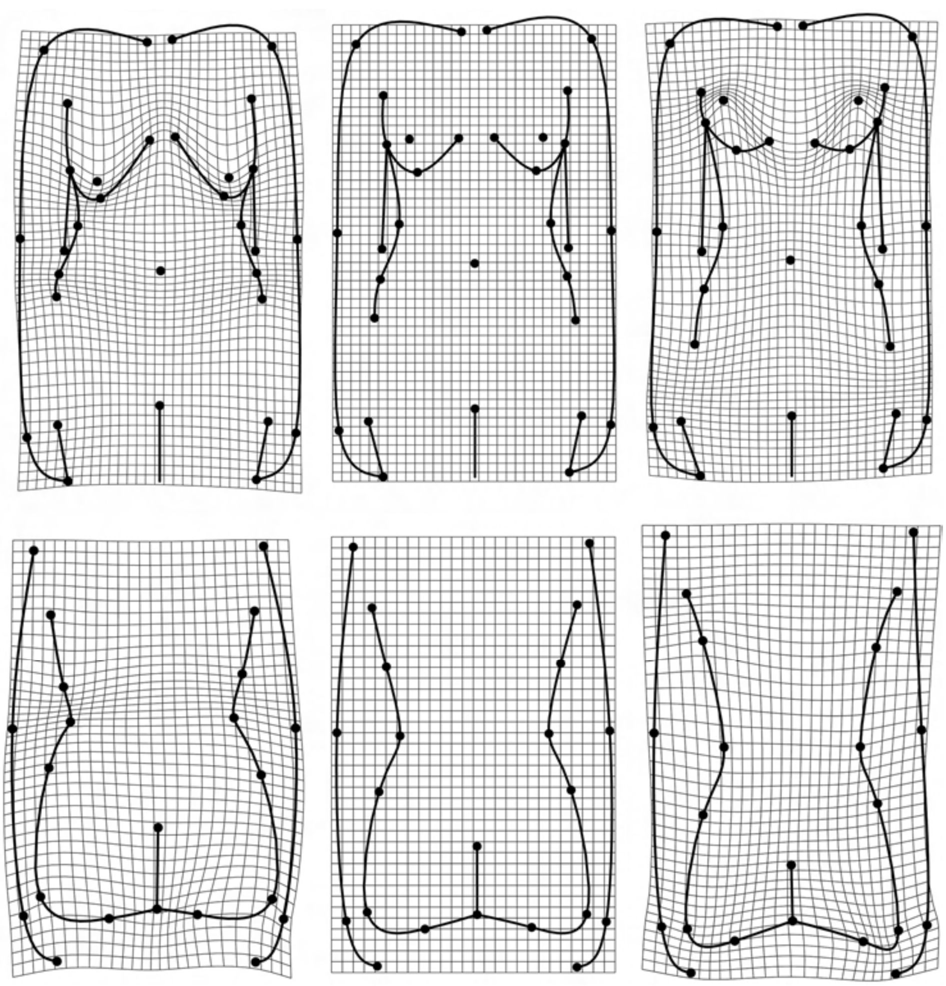

Figure 6:
Visualization of the shape regression on perceived female frontal and back attractiveness by TPS deformation grids. The middle panels show the average landmark configurations (upper row: front view; lower row: back view), the side panels indicate the transformation towards higher (right) and lower (left) perceived attractiveness (deformations corresponding to ±4 units for the front view, and ±7 units for the back view, numbers exceeding the range of the ratings for the sake of an optimal rendering).

pressed for the landmarks that characterize the waist. The opposite is true for the predicted transformation with regard to low attractiveness ratings. These overall dissimilarities do not reflect differences in total body fat (which had been adjusted for via BMI) but rather differences in body fat *distribution*.

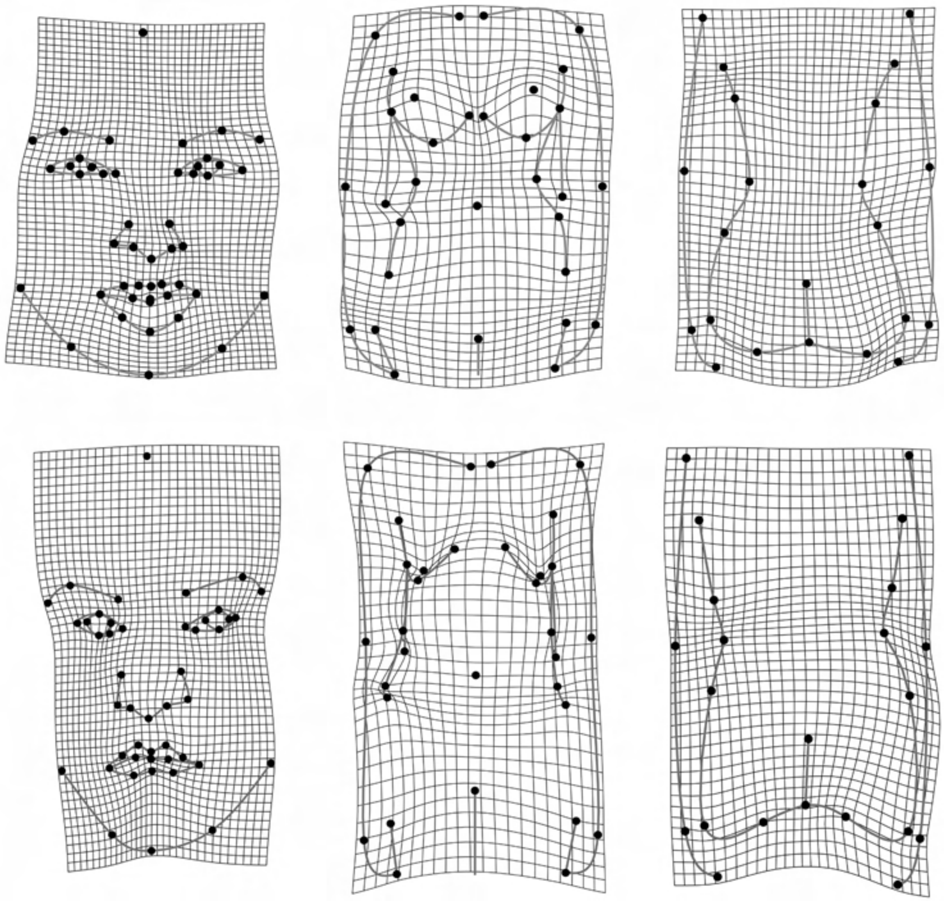

Figure 7:
Adjustment for body mass index in the shape regression upon rated attractiveness for all three body parts. Each pair of TPS grids represents both directions of deformation for the region involved. Upper row: deformation with increasing rated attractiveness; lower row: deformation with decreasing attractiveness.

Discussion

The aim of this study was to ascertain the relationships between perception of women's physical appearance and indicators of developmental stability and hormone markers. Our results generally support this notion. Attractiveness ratings of women's faces and bodies were found to be significantly associated with specific localized shape differences in regions of known E-sensitivity and with the amount of FA.

According to these findings we may be able to trace rated attractiveness back to a single dimension of naturally occurring shape covariation between face, front and back view, because the shape features detected are generally considered to be responsive to the same biological impact, namely the T/E ratio. This could reflect a consistent factor within the body configuration, perhaps corroborating Thornhill and Grammer's (1999) hypothesis that the human face and body together comprise a condition-dependent ornament of mate value. An ornament is an elaborate trait that functions in competition for mates. In empirical studies with both humans and animals, such ornaments are often found to function as honest signaling of phenotypic and genetic quality (Pomiankowski & Iwasa, 1998; van Doorn & Weissing, 2004). On the basis of our results, we may speculate that this also applies to the female body in the way that variation in face and body shape differentially relates to the level of E.

It is known that female body features are closely linked to body fat distribution and fertility (Frisch, 2002). Body fat distribution is maximally sexually dimorphic during early reproductive life (while it is minimal in infancy, childhood, and old age), and is mediated by sex steroids in combination with heritable genetic factors (Nelson *et al*., 1999). This distribution of body fat is thought to signal the ratio of pubertal to adult E/T, and the predominance of E at puberty produces a typical female (gynoid) body shape, while the predominance of T produces a typical male (android) body shape (Björntrop, 1997). However, in order to strengthen its signalling value, body fat must be distributed over prominent places like breasts and buttocks. Otherwise, its signalling value would be lowered and thus it could only effect the biomechanical abilities of the body. Healthy females have higher levels of E/T. Low waist-to-hip ratio (WHR) in women is typically associated with high levels of circulating E, whereas high WHR is correlated with high levels of circulating T (Beck *et al.*, 1976; Evans *et al.*, 1983). Consequently, WHR has been suggested to be an 'honest' signal of an individual's fertility and health. Furthermore, Singh and Zambarano (1997) report that overall weight is linked to fertility: heavier mothers have more children. Appreciation of heavier women in various cultures seems to depend on environmental stability (Anderson *et al*., 1992). In unstable environments, plumpness is linked positively to status and attractiveness. Our study used data from Caucasian women from the U.S.A., which we consider a rather stable environment, and one consequently expects that women that maintain the hourglass body-shape are rated more highly in attractiveness.

Our data indeed reveal that the lower body shape shows the classic gynoid fat distribution in the attractive shapes in contrast to a more android fat distribution with abdominal fat accumulation in the shapes corresponding to decreased attractiveness. This latter distribution is known to be associated with an elevated health risk. Fat stored in the lower half of the body is usually attributed to obesity, or to low estrogen levels which, in turn, may be due to age or to hormonal disregulations. This is often observed in combination with lower fertility and also with increased risk for coronary heart disease (Singh, 1993). Furthermore, body weight in women is known to be positively associated with levels of FA (Manning, 1995). This appears also consistent with regard to female fertility. In another study, Manning and Scutt (1996) found that FA in four paired soft tissue traits showed a marked decrease on the day of ovulation.

Besides being sexually dimorphic, the distribution of body fat is age-dependent. In the populations studied, firm breasts with the axis pointing upward in a V-angle – features associated only with young women – are rated as attractive (Grammer *et al*., 2001). Our data support this assertion since deformation with increasing rated attractiveness results in shape changes mainly in the breast region and in the abdomen (Figure 6, 7). The relationship between asymmetry and breast volume was previously found to show negative allometry, that is, women with large breasts had smaller asymmetry than predicted for their breast size (Manning *et al*., 1997). Furthermore, asymmetric women were found to have also fewer children later in life than symmetric ones. These data again support the view that heavy women with high levels of body fat produce more E and, therefore, bigger breasts. However, since higher E levels lead to an increase in breast asymmetry and are also associated with an increased susceptibility of the immune system (Service, 1998), we may expect that only women with 'good genes' are able to maintain sexually dimorphic characteristics which are sensitive to E and simultaneously to low levels of FA.

A similar trade-off is known for the face – a body feature otherwise clearly differing from the corpus in biological function. Facial FA increases in women exposed to higher titers of E during development (Fink *et al.*, 2004) and we know from several studies that this decreases attractiveness ratings (see for review Thornhill & Gangestad, 1999). Our data reveal that shape changes in the face that are associated with higher attractiveness ratings result in a configuration that appears generally rounder, with a more gracile nose and chin and larger lips – characteristics which are known to be facial E markers (Johnston & Franklin, 1993; Symons, 1995). Likewise, shape changes that relate to decreasing perceived attractiveness resemble in many aspects features linked with the adult male face. Specifically, an overall elongation and a more pronounced lower face are some of the classic sexually dimorphic characteristics in men, linked to extended facial growth (hypermorphosis) and other developmental processes under the influence of T (Enlow, 1996; Rosas & Bastir, 2002; Schaefer *et al*., 2004; Bulygina *et al*., 2006). Such features present in female faces might therefore indicate an E/T ratio shifted towards higher T, and serve to trigger the less favorable physical evaluation we have found in the males' perception.

In conclusion, it seems that the proposed trade-off between effects of sex-steroids on sexually dimorphic features versus maintaining low levels of FA applies not only to the female body but also to the female face. Women in prime condition may better be able to express hormone-dependent physical characteristics that consequently are rated more attractive by men. Our data support, albeit weakly, the notion that the psychological mechanism by which women's physical attractiveness is rated exploits indicators of their hormonal and developmental status. However, mate value is clearly not determined by physiology alone, but embraces a complex array of traits relating to personal, social, and ecological contexts for both men and women. Our study focused on physical appearance and hinted at condition-dependent signaling of the female face and body – factors that play a major role in short-term mating and response "at first sight". Their predictive value for a stable and long-term relationship is still a matter of further investigation.

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