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Testosterone increases perceived dominance but not attractiveness in human males

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Recent evidence suggests that certain features on the human face indicate hormonal levels during growth, and that women judge the attractiveness of potential partners based on the appearance of these features. One entrenched notion is male facial features that are affected by testosterone are used as direct cues in mate preference. Testosterone may be particularly revealing as it is purported to be an honest indicator of male fitness. Increased testosterone may impose an immunocompetence handicap on the bearer and only the best males can carry this handicap. To date, tests of this theory have been indirect, and have relied on digital manipulations that represent unrealistic continuums of masculine and feminine faces. We provide a much more direct test by manipulating digitally male faces to mimic known shape variation, caused by varying levels of testosterone through puberty. We produced a continuum of faces that ranged from low to high levels of testosterone in male faces and asked women to choose the points on the continuum that appeared most attractive and most physically dominant. Our data indicate that high testosterone faces reveal dominance. However, there is no evidence of directional selection for increased (or decreased) testosterone in terms of attractiveness to the opposite sex. We discuss the relevance and applicability of evolutionary interpretations of our data and, contrary to predictions, provide evidence of stabilizing selection acting on testosterone through mate preferences.

Keywords: sexual selection; *Homo sapiens*; immunocompetence; handicap; mate preference

1. INTRODUCTION

Several hypotheses suggest that human faces display markers of hormones, and that these cues affect judgements of facial attractiveness (Johnston & Franklin 1993; Perrett *et al.* 1998; Thornhill & Gangestad 1999; Johnston *et al.* 2001) and dominance (Mazur *et al.* 1994; Mazur & Booth 1998). In particular, evolutionary psychologists have generated theories to predict that levels of testosterone reflected in male facial features are (or were) important in generating sexual dimorphism in humans, as well as directly affecting mate preferences (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Thornhill & Gangestad 1999; Johnston *et al.* 2001). It has been suggested that facial testosterone may be an honest indicator of male fitness (Thornhill & Gangestad 1999), as increased testosterone can impose an immunocompetence handicap on the bearer (see discussions in Grossman 1985; Hasselquist *et al.* 1999; Duckworth *et al.* 2001) and only the best males can carry this handicap (Zahavi 1975; Hamilton & Zuk 1982).

Existing tests of testosterone-related hypotheses of human attractiveness have focused on producing feminine–masculine axes of facial shape in digital representations (by computer graphics manipulations) and monitoring people's responses to these faces (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Johnston *et al.* 2001). In some cases, more masculine, male faces are preferred (Penton-Voak *et al.* 1999; Johnston *et al.* 2001), whereas in others more feminine male faces are judged as attractive (Perrett *et al.* 1998). Part of this variation appears to be correlated with the stage of ovarian cycle of women judging the faces (Penton-Voak *et al.* 1999; Johnston *et al.* 2001). However, there is no evidence to indicate that these fluctuations in female preferences affect actual partner choice.

Previous experiments have also provided fairly unnatural, and rather indirect, tests of the testosterone-related hypotheses. First, there are many differences between masculine and feminine faces, which are not accounted for by testosterone alone (Perrett *et al.* 1998). Hence, the results of these studies are difficult to interpret in terms of testosterone expression in the male face. Second, the faces produced through such manipulations result in male facial shapes outside a natural male distribution (Penton-Voak *et al.* 1999; Johnston *et al.* 2001), and are commonly presented as faces without hairlines or necks (Perrett *et al.* 1998). Preferences for face shapes from such artificial distributions may not reflect preferences shown in society, as the facial variation in normal male human populations can be very different.

A more direct approach to testing testosterone-related hypotheses is to produce facial variation that reflects quantified variation in testosterone levels. Therefore, we manipulated the shape of male faces to mimic growth differences resulting from varying levels of testosterone during puberty. Women viewed these faces and made judgements of facial attractiveness and dominance. According to previous reports, we predicted that women should find faces with higher testosterone expression most attractive (Thornhill & Gangestad 1999).

2. MATERIAL AND METHODS

We took digital photographs of 21 male Caucasians' faces in a (right-side) profile and face-on orientation to the camera. Models were 18–21 years old, had short hair, lacked beards or

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Table 1. Approximate relative trait size changes (i.e. distances between two points) resulting from warp manipulations for the 100% high and 100% low testosterone treatments, for profile and face-on photographs of male faces.
(Facial characters were determined from anthropometric definitions (Farkas 1981) and their position was estimated on each male face. Points used were: nasion (N) midpoint of both nasal root and nasofrontal suture; pogonion (POG) anterior midpoint of the chin; gonion (GO) most lateral point of the mandibular angle; menton (ME) lowest point on the mandible; ans (ANS) approximated by the posterior extremity of the nose; articulare (ART) estimated by the posterior and ventral attachment of the ear; sella (S) estimated by the anterior and ventral attachment of the ear.)

	profile		face-on	
trait	100% high	100% low	100% high	100% low
N–ANS	+0.01	−0.01	+0.01	−0.01
N–ME	+0.01	−0.01	+0.01	−0.01
ART–ANS	+0.01	−0.01	0	0
ART–POG	+0.02	−0.02	+0.02	−0.02
ART–GO	+0.04	−0.04	+0.04	−0.04
S–ME	+0.02	−0.02	+0.02	−0.02
ART–ME	+0.02	−0.02	+0.02	−0.02
GO–POG	+0.02	−0.02	+0.01	−0.01

moustaches, were not wearing jewellery, and were told to adopt a neutral facial expression while sitting for the photographs. Photographs were taken in standardized lighting conditions against a common background.

We compared how facial structure changes with natural levels of testosterone during puberty, and in delayed puberty boys treated with low-dose testosterone (Verdonck 1997; Verdonck *et al.* 1999) to create vectors of facial trait changes that represent realistic variation in plasma testosterone influencing facial bone growth fields (Enlow 1990; Silveira *et al.* 1992). The relative changes of the facial traits we manipulated are listed in table 1. Briefly, face height increased and the lower jaw became larger with increased testosterone. These manipulations were specifically designed to isolate the effects of testosterone on facial skeletal characters, providing a more direct test of the effects of testosterone on perception of the face.

We used the warp function in Gryphon Software's Morph program to alter the shape of male faces according to the trait size changes listed in table 1. We also digitized 10 points around the eyes, five on the nose, and five on the lips to ensure that this part of the face did not change under the warp manipulation. The warp function moves the reference points to a specified position without altering colour or tone (figure 1). In addition to producing the high and low testosterone treatments, we produced nine, equally spaced, intermediate warps between the control and high testosterone faces, and between the control and low testosterone faces. This resulted in 21 representations of a single face that ranged from the low treatment to the high treatment with equal warp differences between all images, and where the median face was the control (i.e. non-manipulated face).

The sequence of 21 representations was arranged in ascending or descending order in a PowerPoint presentation, with one image on each slide. For half the faces the first slide contained the lowest testosterone treatment; for the remaining faces the first slide was the highest testosterone treatment. Each slide also displayed a sequential number so that viewers could tell us which slide they chose.

Thirty females, age 18–21 years old, viewed each of the 42 sequences on a computer screen. Subjects were asked to choose the most sexually attractive, and most physically dominant looking, face in each sequence. One of the experimenters advanced (or went back through) the slides at a regular pace of one slide approximately every 0.5 s. In addition, viewers instructed the experimenter to advance, reverse, and stop the sequence whenever the viewer wished. The order of male faces viewed by females was randomized, except that all the profile faces were presented in sequence, as were the face-on presentations. Half of the viewers saw the profile sequences first, and vice versa. Viewers were paid for their participation. If a viewer recognized one of the male faces, she informed the researchers and the data for that face were discarded.

3. RESULTS AND DISCUSSION

The frames chosen by females as being most attractive, for both face-on and profile views, were faces with testosterone expression very similar to that of the non-manipulated face (paired *t*-tests of the most attractive versus the control face: face-on, $t_{20} = 1.94$, $p = 0.067$; profile, $t_{20} = 1.86$, $p = 0.078$). The frequency diagram of most attractive frame choice illustrates that women's preferences centre on existing levels of testosterone in men's faces (figure 2). Such distributions are consistent with stabilizing selection acting on testosterone expression in men's faces rather than the previously proposed directional selection for reduced or increased testosterone (Perrett *et al.* 1998; Johnston *et al.* 2001).

It is important to point out that individual female raters used the entire range of faces for attractiveness choices. For face-on views, the mean ± s.e. (among-rater) range of frame chosen was 18.63 ± 0.54 (out of a possible 21) for face-on views, and 19.50 ± 2.54 for profile views. This indicates that females did not feel constrained to only using the central portion of the animation sequences, and that our result is not an artefact of a rater central tendency independent of attractiveness judgements.

In order to explore further the effects of testosterone on facial attractiveness, we calculated an index of testosterone in non-manipulated male faces (the ratio of ART–POG length to N–S length, where a high value indicates higher facial testosterone expression; see table 1 for definitions) and examined whether natural variation in testosterone affected choice of frames. Linear measurements were taken directly from the digital photographs of profile faces.

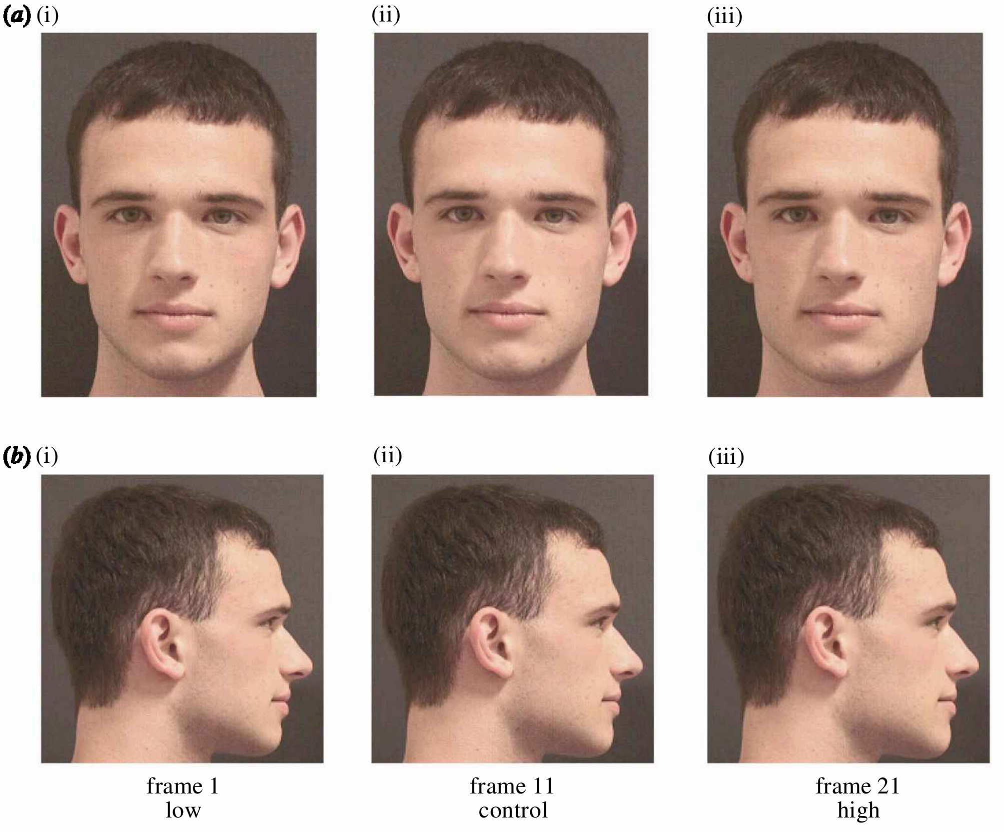

Figure 1. The extremes of the manipulations produced for (a(i)–(iii)) face-on and (b(i)–(iii)) profile views of the same face. Low, low testosterone treatment; control, unmanipulated face; high, high testosterone treatment.

Natural levels of facial testosterone were negatively correlated with choice of attractive frame (face-on: Pearson $r = -0.636$, $n = 21$, $p = 0.0011$; profile: $r = -0.710$, $n = 21$, $p = 0.000\ 15$). Inspection of the numerical values of these correlations indicated that the most preferred versions of naturally high testosterone faces were those that reduced apparent testosterone. Whereas the most preferred representations of naturally low testosterone faces were those that increased apparent testosterone. The net effect of such preferences is a convergent selection pressure on average testosterone expression across the population, which provides further evidence of stabilizing selection on testosterone. Although these correlations are strong, we need to emphasize that there is a possibility that raters' preferences could alter with their oestrus cycle (cf. Penton-Voak *et al.* 1999; Johnston *et al.* 2001). In further studies, it would be interesting to investigate whether females' preferences for facial testosterone change systematically according to the possibility of conception.

The choice of the most dominant frame was very different to the choice of the most attractive frame. In agreement with previous evidence (Perrett *et al.* 1998; Johnston *et al.* 2001), the most dominant frames were those with a high degree of testosterone expression (figure 2). This pattern helps to confirm that our manipulation was realistic, as links between testosterone and male aggression and dominance are generally well supported (Mazur & Booth 1998).

It was also evident that choices made by viewers when judging males face-on were different to when males were in profile. Females chose faces significantly higher in testosterone as most attractive when viewing a face in profile, compared with the same male face-on ($t_{20} = 3.16$, $p = 0.0049$). Conversely, females chose faces significantly lower in testosterone as most dominant for profile, versus face-on, views of males ($t_{20} = 3.65$, $p = 0.0016$). These differences clearly demonstrate that female judgement of a male face changes with viewing angle. This implies that further experiments need to account for three-dimensional viewing of faces if researchers are going to document realistic relations between facial characters and socially (or evolutionarily) important parameters. However, in the context of our experiment, we observed the same general relationships between attractiveness (or dominance) and facial testosterone expression in profile and face-on.

A recent resurgence in adaptive explanations of human behaviour and morphology has stimulated interest in whether researchers can demonstrate evolutionarily important relationships through preference and rating experiments (Perrett *et al.* 1998; Scheib *et al.* 1999; Johnston *et al.* 2001). To demonstrate a current evolutionary effect a research programme must meet certain criteria. In the context of this study, we would need to demonstrate evidence of selection pressure acting on traits, and heritable variation in those traits. In terms of the former, our data could indicate stabilizing selection if there is a link between differential reproductive success and rating of facial attractiveness. There is evidence that facial attractiveness positively affects the ways in which others treat them in many social contexts (Kalick 1988; Zebrowitz 1997). However, links between facial attractiveness and health or reproductive success are equivocal or non-existent (Kalick *et al.* 1998; Shackelford & Larsen 1999; Rhodes *et al.* 2001). Women may place less importance

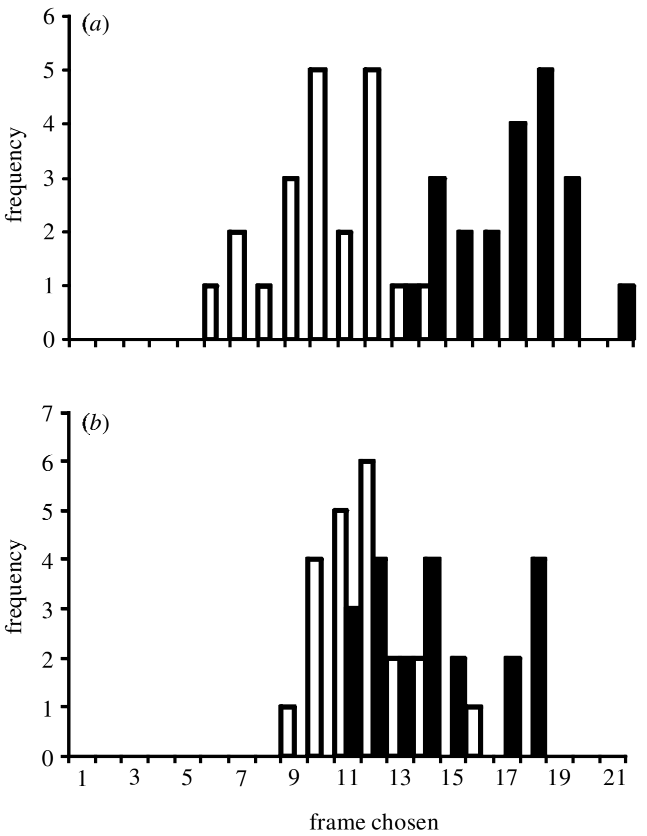

Figure 2. (*a*) Frequency histogram for frame choice of most attractive (open bars) and most dominant (filled bars) frames for face-on views; (*b*) and for profile views of male faces. In both distributions, the choice of dominant frame represented a much higher degree of testosterone expression than the choice of attractive frame (face-on, $t_{20} = 11.75$, $p < 0.001$; profile, $t_{20} = 3.05$, $p = 0.0064$).

on physical attractiveness when choosing a mate than men do (Waynforth 2001). This implies a low probability that male facial attractiveness will relate to reproductive success or fitness. However, it does not preclude that attractiveness was related to reproductive success at some time in our evolutionary history. There is some indication that increased facial dominance is associated with increased sexual activity in young men (Mazur *et al.* 1994), but increased sexual activity does not necessarily result in increased numbers of offspring (Mueller & Mazur 1998). Additionally, extreme dominance can negatively influence reproductive success (Mueller & Mazur 1998).

In terms of the 'heritability' criteria, there is some evidence of significant heritability of the male facial traits we assessed (upper estimates range from 10% to 36% heritability) (Enlow 1990) and of circulating testosterone levels in men (upper estimates of *ca.* 60% heritability) (Harris *et al.* 1998). Overall, interpreting our experiment and those using similar methodologies (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Scheib *et al.* 1999; Johnston *et al.* 2001) in terms of evolutionary processes is problematic, and generally unsupported by empirical evidence. It is more likely that judgements of particular facial shapes are mediated by cultural norms and individual decision-making (Tooby & Cosmides 1989).

Even if some researchers insist on evolutionary interpretations, we cannot find evidence for directional selection to reduce or increase testosterone through female preferences. Previous studies that have documented female preferences for masculine (Johnston *et al.* 2001) or feminine (Perrett *et al.* 1998) male faces cannot be interpreted in terms of the effects of testosterone alone. Other hormonal differences between the sexes must (in part) explain previously documented preferences. It may be that selection acting on oestrogen and on female faces may equally explain human evolutionary changes (Thornhill & Grammer 1999). The comparative literature has demonstrated that both sexes can be the target of directional sexual selection and that both sexes change through evolutionary time, resulting in dimorphism (Karubian & Swaddle 2001). Our data also suggest that social dominance may underlie the evolution of human sexual dimorphism, as increased testosterone is positively associated with perceived dominance. However, increased perceived dominance does not enhance male attractiveness.

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