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## Testosterone responses to competition in men are related to facial masculinity

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Relationships between androgens and the size of sexually dimorphic male traits have been demonstrated in several non-human species. It is often assumed that a similar relationship exists for human male faces, but clear evidence of an association between circulating testosterone levels and the size of masculine facial traits in adulthood is absent. Here we demonstrate that, after experimentally determined success in a competitive task, men with more a masculine facial structure show higher levels of circulating testosterone than men with less masculine faces. In participants randomly allocated to a 'winning' condition, testosterone was elevated relative to pre-task levels at 5 and 20 min post-task. In a control group of participants allocated to a 'losing' condition there were no significant differences between pre- and post-task testosterone. An index of facial masculinity based on the measurement of sexually dimorphic facial traits was not associated with pre-task (baseline) testosterone levels, but was associated with testosterone levels 5 and 20 min after success in the competitive task. These findings indicate that a man's facial structure may afford important information about the functioning of his endocrine system.

**Keywords:** testosterone; facial masculinity; competition; sexual dimorphism

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## 1. INTRODUCTION

Testosterone-dependent secondary sexual characteristics are demonstrably important in mate choice (Andersson 1994). Relationships between androgens and sexual displays have been demonstrated in several non-human species (Roberts *et al.* 2004), and it has been proposed that a similar underlying biological process may be useful in explaining women's preferences for sexually dimorphic facial characteristics in men (see Rhodes 2006, for a review). A crucial underlying assumption of much work investigating women's preferences for sexually dimorphic facial traits is the existence of a relationship between circulating testosterone levels and facial masculinity. Testosterone administration causes craniofacial growth in adolescents (Verdonck *et al.* 1999), but direct evidence of an association between circulating testosterone levels and masculine facial trait size in adulthood is absent. Moreover, evidence for an association between circulating testosterone levels and perceived masculinity in adult male faces is equivocal (Neave *et al.* 2003; Penton-Voak & Chen 2004; Roney *et al.* 2006).

To date, studies investigating relationships between appearance and testosterone (Neave *et al.* 2003; Penton-Voak & Chen 2004; Roney *et al.* 2006) have used a single measure of testosterone from each participant, failing to take into account that testosterone levels in men are dynamic, exhibiting both diurnal variability and fluctuations in response to social and psychological events. For example, circulating testosterone levels in men are affected by watching arousing videos (Hellhammer *et al.* 1985), brief interactions with women (Roney *et al.* 2003, 2007) and being insulted (Cohen *et al.* 1996). Moreover, Neave *et al.* (2003), Penton-Voak & Chen (2004) and Roney *et al.* (2006) did not control for salivary blood contamination that can elevate salivary testosterone levels (Kivlighan *et al.* 2004) and could introduce unsystematic error, or even systematic bias if its causes (e.g. gingivitis and/or micro-injury to the oral mucosa) vary systematically with other participant characteristics.

Given that testosterone levels are dynamic, total tissue exposure to the hormone's masculinising effects may depend on the magnitude of hormonal responses to events and not just baseline levels, e.g. average plasma testosterone concentrations over time may be more closely associated with post-event testosterone levels than with baseline levels. Analogous evidence exists with respect to the importance of blood glucose dynamics. Although chronic hyperglycaemia, due to elevated baseline (fasting) blood glucose, is a continuous risk factor for cardiovascular disease (Coutinho *et al.* 1999) and microvascular complications (Stratton *et al.* 2000), postprandial hyperglycaemia is an independent risk factor (Ceriello 2000). In type 2 diabetes patients, glycosylated haemoglobin levels (HbA<sub>1c</sub>), which reflect average blood glucose concentrations over time, are more closely associated with postprandial plasma glucose, than with fasting or preprandial levels (Avignon *et al.* 1997). Moreover, coronary heart disease (Donahue *et al.* 1987) and mortality (DECODE 1999) are better predicted by postprandial than fasting plasma glucose.

Consistent with the 'challenge hypothesis' (Wingfield *et al.* 1990) men respond to competitive situations with increased testosterone levels (for a review see Archer 2006). In men, testosterone levels are affected by the outcome of competition, increasing in winners relative to losers in physical (Mazur & Lamb 1990) and non-physical (Gladue *et al.* 1989; Mazur *et al.* 1992; McCaul *et al.* 1992) contests. In certain circumstances, testosterone levels rise in anticipation of a contest (e.g. Booth *et al.* 1989; Mazur *et al.* 1992). Moreover, direct participation in competition is not necessary to elicit testosterone responses since

vicarious experiences of winning and losing can have similar effects (Bernhardt *et al.* 1998). There is some evidence for individual differences between men in the magnitude of their testosterone responses to contests (Cohen *et al.* 1996; Edwards *et al.* 2005), and the present experiment was conducted to determine whether such individual differences are related to an aspect of anatomical masculinization, i.e. the expression of sexually dimorphic characteristics in the face.

There is evidence that individual differences in behavioural responses to certain stimuli are associated with another anatomical trait, second-to-fourth digit ratio (2D:4D), which is sexually dimorphic (Manning *et al.* 2000) and a putative marker for prenatal testosterone (Manning 2002). Millet & Dewitte (2007) found that, after viewing an 'aggressive' music video, men with more masculine (lower) 2D:4D ratios gave more aggressive responses to a series of hypothetical provocation scenarios. Similarly, Van den Bergh & Dewitte (2006) found that exposure to images of attractive women produced more pronounced changes in behaviour in an ultimatum game in men with masculine (lower) 2D:4D ratios. Neither study, however, measured testosterone levels and metaanalysis has indicated that in the normal adult population 2D:4D is not associated with circulating testosterone levels (Hönekopp *et al.* 2007). Moreover, 2D:4D is unrelated to facialmetric measures of masculinity in men (Burriss *et al.* 2007). Crucially, then, definitive evidence of an association between circulating testosterone and facial masculinization in adult men has yet to be found, even though a large literature on human facial preferences is based on this assumption (see Rhodes 2006 for a review).

Previous research using a variety of procedures has demonstrated that participation in competition increases testosterone levels, and these increases tend to be greater in winners than in losers (for a review see Archer 2006). Consequently, the *a priori* aim of this research was to examine the associations between facial structure and the magnitude of the testosterone increases that occur in response to success in competition. Accordingly, we tested whether there was an association between an index of facial masculinity (derived from measurements of sexually dimorphic facial characteristics) and the magnitude of men's testosterone responses to success in a competitive task. We used a task similar to that used by Gladue *et al.* (1989), i.e. a non-physical laboratory contest in which participants are experimentally allocated to either a winning or losing condition by adjusting feedback regarding task performance. However, the task used in the present study also involved an element of vicarious participation in a contest, since participants were asked to predict the outcome of wrestling bouts.

## **2. MATERIAL AND METHODS**

### ***(a) Measurement of salivary testosterone and blood contamination***

Male participants ( $n = 57$ ; mean age  $21.7 \pm 2.5$  years) each provided a series of saliva specimens, two before and two after participating in a competitive task according to a schedule similar to that used by Mazur *et al.* (1997). Specimens were collected at 10 ( $T_1$ ) and 5 ( $T_2$ ) min before participating in the task, and 5 ( $T_3$ ) and 20 ( $T_4$ ) min after completing the task. The competitive task took approximately 5 min to complete. To avoid anticipatory effects on testosterone levels (e.g. Booth *et al.* 1989; Mazur *et al.* 1992, 1997), the competitive aspect of the task was explained fully to participants after they had provided their second saliva specimen ( $T_2 - 5$  min before the task). All participants were tested in isolation. To minimize variability due to diurnal fluctuations in circulating testosterone

(Dabbs 1990), all experimental sessions took place between 12.30 and 16.00, and for the specimens collected for this experiment there were no significant associations between testosterone concentrations and specimen production times. To stimulate saliva production, participants chewed sugar-free gum and then delivered 5 ml saliva into a polypropylene cryotube (Nalge Nunc International, Rochester, NY). Specimens were frozen and stored at -20°C and then assayed in duplicate using a competitive enzyme immunoassay for testosterone (Salimetrics LLC, State College, PA). The average intra-assay coefficient of variation was 8.9% and inter-assay coefficient was 10.3%. To assess blood contamination, a competitive enzyme immunoassay (Salimetrics LLC) was used to determine levels of transferrin in each saliva specimen. For this, the average intra-assay coefficient of variation was 6.5% and inter-assay coefficient was 5.5%.

### **(b) Competitive task**

The competitive task involved predicting the outcome of Sumo wrestling bouts based on fictitious information about the wrestlers. The task involved notional direct competition with other participants (to be most successful in predicting the outcome of bouts) and vicarious experiences of being involved in competition (watching a chosen wrestler compete). Success or failure (i.e. 'winning' or 'losing') in the task was experimentally determined. Of the 57 participants, 10 were selected randomly and allocated to a losing control group while the remaining 47 were allocated to a winning condition. Allocation to the losing group was limited since the purpose of this control group was simply to validate the experimental procedure (i.e. demonstrate that participation in the task caused changes in the testosterone levels). The main aim of this research was to examine the associations between facial structure and that magnitude of the testosterone increases that occur in response to success in competition, rather than compare associations between testosterone and facial structure in experimentally allocated 'winners' and 'losers'.

Stimuli were presented on a computer monitor, and during the task participants were asked to predict the outcome of a series of six wrestling (Sumo) bouts based on information about the wrestlers (e.g. height, weight, reach) who were identified by letter codes. After making each prediction, participants were shown a short (< 30s) video of a Sumo bout with audio commentary. Prior to the start of each bout, an arrow was used to label a wrestler as the one chosen by the participant. However, a participant's success or failure in predicting the outcome was experimentally allocated with either the winning or losing wrestler marked as chosen. Wrestlers were distinguishable by the colour of their mawashi (belt worn by each wrestler). In the winning condition, participants were told, and shown videos indicating, that they had successfully predicted the outcome of five out of six bouts. In the losing condition, the success rate given was just one out of six bouts.

### **(c) Facial masculinity index**

Participants' faces were photographed in a standing position, with a neutral expression, using a digital camera (Canon EOS 350D) at a resolution of 1629 x 2304 pixels, with bilateral illumination (Portaflash DL 1000). Where necessary to reveal the hairline, hair was pulled back with a hairband. Five facial dimensions (ratios) previously shown to be sexually dimorphic (Penton-Voak *et al.* 2001) were measured. These ratios were: (i) eye size (horizontal inter-exocanthial distance/inter-endocanthial distance), (ii) lower face/face height (vertical distance from mean pupil height to gnathion approximation/vertical distance from trichion to gnathion approximation), (iii) cheekbone prominence (horizontal

distance between most outward projecting points on the face at or below the eyes/horizontal distance between left and right gonion approximations), (iv) face width/lower face height (horizontal distance between most outward projecting points on the face at or below the eyes/vertical distance from mean pupil height to gnathion approximation), and (v) mean eyebrow height (mean vertical distance from pupil to inferior aspect of brow/vertical distance from trichion to gnathion approximation). Measurements were made as previously described (Penton-Voak *et al.* 2001) using University of Texas Health Science Center, San Antonio (UTHSCSA) ImageTool to record landmark locations.

For each dimension, measures were converted to standardized (*z*) scores and a composite facial masculinity index was computed as the sum of these *z*-scores (oriented such that high scores are masculine for each dimension). Measurements were made in duplicate by two independent research assistants blind to the testosterone status of the participants. The duplicate measurements were highly correlated ( $r = 0.98$ ) and the mean of these was used in analyses.

#### **(d) Perceived masculinity and dominance ratings**

An independent sample of 72 raters (61 females and 11 males; mean age 19.2 years; s.d. 2.7 years) rated the participants' faces for perceived masculinity. A further sample of 29 raters (18 females and 11 males; mean age 24.8 years; s.d. 6.9 years) rated the faces for perceived dominance. Digital photographs were cropped to remove hair and clothing and then presented to raters in random order on a computer screen. Raters were asked to rate each face on a 7-point Likert scale from 1 (not at all masculine/dominant) to 7 (very masculine/dominant). Raters exhibited a high degree of consensus for perceived masculinity (Cronbach's  $\alpha = 0.96$ ) and dominance ( $\alpha = 0.85$ ), so mean ratings for each face were used in analyses.

#### **(e) Statistical analyses**

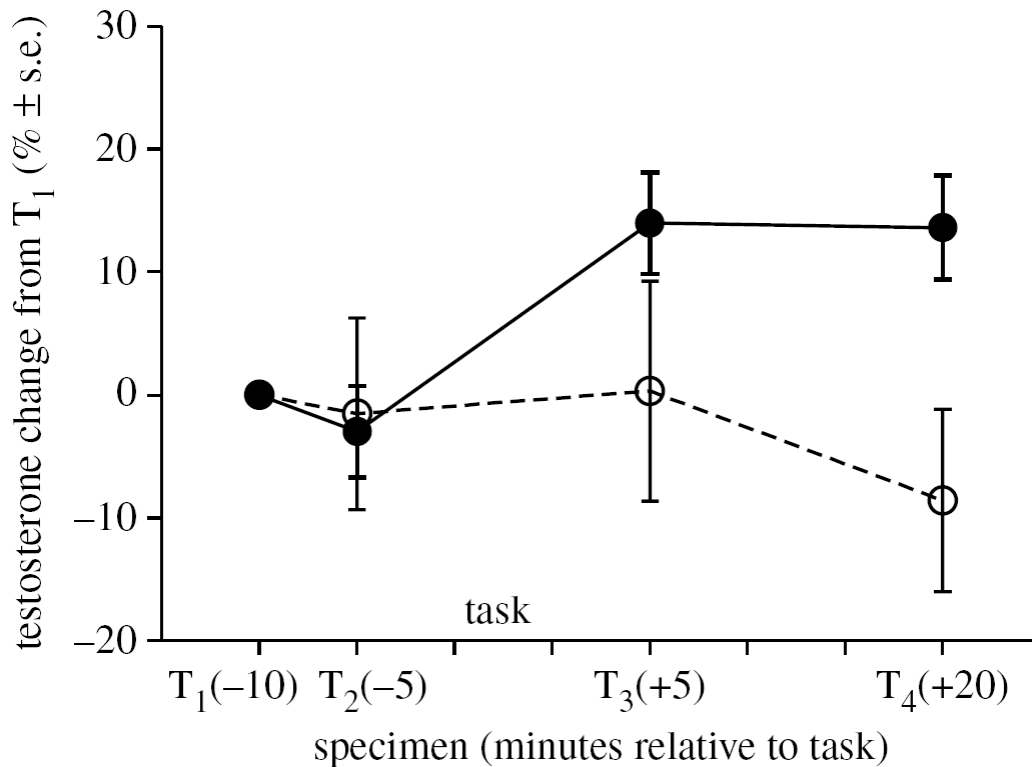
Since testosterone concentrations vary across an order of magnitude (34 – 247 pg ml<sup>-1</sup> in the present study) and are positively skewed (skewness/standard error of skewness greater than 2), statistical tests involving testosterone concentrations have been performed on log-transformed values. All analyses were carried out using SPSS 13.0. To validate the experimental task (i.e. to determine whether being allocated to the winning condition caused an increase in testosterone), mean pre-task ( $T_1$  and  $T_2$ ) and post-task ( $T_3$  and  $T_4$ ) testosterone levels were calculated for each participant and analysed using a 2 (win/lose) x 2 (pre/post) repeated-measures ANOVA. *Post hoc* comparisons between mean pre-task ( $T_1$  and  $T_2$ ) and post-task testosterone levels were conducted using paired sample *t*-tests. All tests were two tailed with  $\alpha = 0.05$ . Pearson product-moment correlation coefficients were calculated to assess zero-order relationships between testosterone levels and both the facial masculinity index and masculinity/dominance ratings. In addition, partial correlation coefficients were calculated to examine linear relationships between variables while controlling for the level of blood contamination in the specimens concerned.

### **3. RESULTS**

#### **(a) Facial masculinity index and testosterone**

Participation in the competitive task affected testosterone levels (figure 1). Overall, in winners ( $n = 47$ ), post-task testosterone (mean  $T_3$  and  $T_4$ ) was on average 14.6 per cent

higher than pre-task testosterone (mean  $T_1$  and  $T_2$ ), while in the control group of losers ( $n = 10$ ) it was 3.3 per cent lower. This condition (win/lose)  $\times$  specimen time (pre/post) interaction was significant (repeated-measures ANOVA,  $d.f. = 1.55$ ;  $F = 4.59$ ;  $p = 0.037$ ). Paired sample t-tests revealed that post-task testosterone (mean  $T_3$  and  $T_4$ ) was significantly higher than pre-task testosterone (mean  $T_1$  and  $T_2$ ) in winners ( $t = 3.45$ ,  $d.f. = 46$ ,  $p = 0.0012$ ). Significant elevation relative to pre-task (mean  $T_1$  and  $T_2$ ) was seen at both  $T_3$  ( $t = 3.59$ ,  $d.f. = 46$ ,  $p = 0.00081$ ) and  $T_4$  ( $t = 2.79$ ,  $d.f. = 46$ ,  $p = 0.0077$ ). In the control group of losers there were no significant differences between pre- and post-task testosterone.



**Figure 1.** Effects of participation in the competitive task on circulating testosterone levels in men experimentally allocated to 'winning' (filled circles,  $n = 47$ ) and 'losing' (open circles,  $n = 10$ ) conditions.

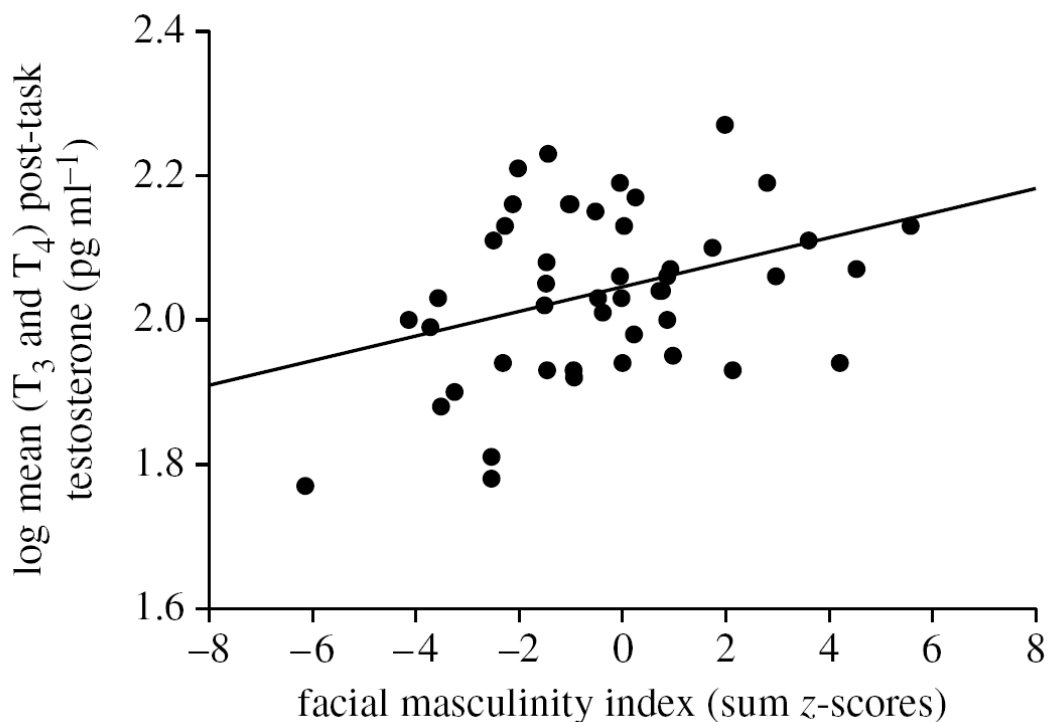
As shown in table 1, in winners ( $n = 47$ ) the facial masculinity index was not associated with pre-task testosterone levels (mean  $T_1$  and  $T_2$ ) but as shown in figure 2, it was positively associated ( $r = 0.36$ ,  $n = 47$ ,  $p = 0.013$ ) with post-task testosterone (mean  $T_3$  and  $T_4$ ). The association was present for specimens collected at  $T_3 - 5$  min ( $r = 0.39$ ,  $n = 47$ ,  $p = 0.006$ ) and  $T_4 - 20$  min ( $r = 0.29$ ,  $n = 47$ ,  $p = 0.048$ ) after the competitive task. Additionally, controlling for blood contamination, partial correlations between the facial masculinity index and testosterone remained significant at  $T_3 - 5$  min (partial correlation  $r = 0.37$ ,  $d.f. = 44$ ,  $p = 0.011$ ) and  $T_4 - 20$  min (partial correlation  $r = 0.31$ ,  $d.f. = 44$ ,  $p = 0.029$ ).

The purpose of allocating 10 participants to a losing condition was simply to create a control group to validate the experimental procedure (i.e. demonstrate that participation caused changes in testosterone levels). Consequently, there were not sufficient men in this group ( $n = 10$ ) to effectively examine associations between facial structure and testosterone

levels after losing. However, it is worth noting that there were no significant associations between the facial masculinity and either pre- or post-task testosterone in losers (all  $p > 0.2$ ). Moreover, while there was a significant zero-order correlation between mean pre-task testosterone and the facial masculinity index for the sample as a whole ( $r = 0.27, n = 57, p < 0.05$ ), once blood contamination was controlled for the partial correlation was non-significant ( $p > 0.05$ ).

**Table 1.** Associations between facial masculinity index and measures of pre- and post-task testosterone (log transformed) for men allocated to the ‘winning’ condition.

	Correlation with facial masculinity index ( $n = 47$ )	Partial correlation with facial masculinity index controlling for blood contamination ( $n = 47$ )
Mean-pre task testosterone	$r = 0.19$ ; NS	$r = 0.20$ ; NS
$T_1$	$r = 0.23$ ; NS	$r = 0.24$ ; NS
$T_2$	$r = 0.14$ ; NS	$r = 0.14$ ; NS
Mean post-task testosterone	$r = 0.36$ ; $p = 0.013$	$r = 0.37$ ; $p = 0.011$
$T_3$	$r = 0.39$ ; $p = 0.006$	$r = 0.40$ ; $p = 0.006$
$T_4$	$r = 0.29$ ; $p = 0.048$	$r = 0.31$ ; $p = 0.029$



**Figure 2.** Association between post-task testosterone (mean  $T_3$  and  $T_4$ ) and facial masculinity index for men allocated to the ‘winning’ condition;  $r = 0.36$ ;  $p = 0.013$ .

### **(b) Perceived masculinity, dominance and testosterone**

For the sample as a whole, neither perceived masculinity ( $r = 0.25$ ,  $n = 57$ ,  $p = 0.06$ ) nor dominance ( $r = 0.21$ ,  $n = 57$ ,  $p = 0.11$ ) was significantly associated with mean pre-task testosterone levels (mean  $T_1$  and  $T_2$ ). Perceived masculinity was not associated with mean post-task testosterone (mean  $T_3$  and  $T_4$ ) in winners ( $r = 0.28$ ,  $n = 47$ ,  $p = 0.06$ ) or losers ( $r = 0.20$ ,  $n = 10$ ,  $p = 0.59$ ). Moreover, perceived dominance was also not associated with mean post-task testosterone (mean  $T_3$  and  $T_4$ ) in winners ( $r = 0.23$ ,  $n = 47$ ,  $p = 0.11$ ) or losers ( $r = 0.26$ ,  $n = 10$ ,  $p = 0.46$ ). These associations remained nonsignificant ( $p > 0.05$ ) controlling for blood contamination in the relevant specimens. There was a significant association between mean blood contamination across specimens  $T_1$ - $T_4$  and perceived dominance ( $r = 0.29$ ,  $n = 57$ ,  $p < 0.05$ ) and a similar association with perceived masculinity approached significance ( $r = 0.26$ ,  $n = 57$ ,  $p = 0.052$ ). Perceived masculinity and dominance ratings were highly correlated ( $r = 0.82$ ,  $n = 57$ ,  $p < 0.0001$ ). However, neither perceived masculinity ( $r = 0.25$ ,  $n = 57$ ,  $p = 0.06$ ) nor dominance ( $r = 0.18$ ,  $n = 57$ ,  $p = 0.17$ ) was significantly associated with the facial masculinity index.

## **4. DISCUSSION**

The present study provides clear evidence of an association between circulating levels of testosterone and facial structure in young adulthood. Since testosterone causes craniofacial growth (Verdonck *et al.* 1999), exposure over time to large and frequent testosterone responses to competitive situations could produce greater cumulative exposure in facial tissues to the hormone's masculinising effects leading to an association analogous to that which exists between postprandial blood glucose spikes and tissue damage. Intermittent spikes in hormone levels may have more pronounced effects than chronic elevation of baseline levels, to which rapid tissue habituation may occur. The fact that the observed association is only present for testosterone levels measured after success in a competitive task demonstrates the importance of studying testosterone dynamics and not just baseline levels.

The lack of significant associations between testosterone measures and either perceived masculinity or dominance is consistent with the findings of Neave *et al.* (2003) but not with more recent findings (Penton-Voak & Chen 2004; Roney *et al.* 2006). Associations in the range 0.2–0.3 were found but they merely approached significance. To place the present findings in context, the three previous studies involved sample sizes of  $n = 48$ , 50 and 38, respectively. The present study, with a sample size of  $n = 57$ , had power of 85.3 per cent to detect a positive association between baseline testosterone and perceived masculinity of the magnitude ( $r = 0.34$ ) reported by Roney *et al.* (2006). Moreover, the present study involved the collection of multiple specimens and statistical control for levels of blood contamination. Given the observed association between perceived dominance and blood contamination, previous reports of associations between perceived masculinity/dominance and baseline testosterone could be blood contamination artefacts, or the discrepant findings could be attributable to endocrine differences between study populations.

The issue as to whether there is an association between testosterone and perceived masculinity still remains rather equivocal, potentially raising some questions about the validity of perceived masculinity measures to assess measured, structural facial sexual dimorphism. Although structural and rated masculinity share some characteristics (DeBruine *et al.* 2006), our data indicate that they are not always interchangeable concepts. Neither



perceived masculinity nor dominance was significantly associated with the facial masculinity index. One possibility is that raters may attribute 'masculine' ratings to faces they find attractive irrespective of the objective sexual dimorphism, due to stereotypical associations between the term 'masculinity' and attractiveness.

These findings confirm an important underlying assumption of current biological theories of male facial attractiveness in humans. Female preferences for masculinity in male faces vary systematically across the menstrual cycle (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001; Jones *et al.* 2005; Welling *et al.* 2007; Roney & Simmons 2008), according to self-perceived (Little *et al.* 2001) and other rated (Penton-Voak *et al.* 2003) attractiveness, female partnership status (Little *et al.* 2002), female sex drive (Welling *et al.* 2008), hypothetical environmental 'harshness' (Little *et al.* 2007) and female waist-to-hip ratio (Penton-Voak *et al.* 2003). Since testosterone can have deleterious effects on the immune system in humans and other mammals (Angele *et al.* 2000; Messingham *et al.* 2001), sexually dimorphic traits (such as masculine facial features) may signal immunocompetence and developmental stability to potential mates (Folstad & Karter 1992). In light of such models, systematic variation in female preferences for masculinity in male faces have been argued to represent adaptive strategic pluralism in mate choice in which cues to immunocompetence (i.e. androgen-dependent dimorphic facial traits) are traded off against cues to prosociality that are associated with low testosterone (Ganges tad & Simpson 2000; Penton-Voak & Perrett 2001).

Hönekopp *et al.* (2007) noted that apparent associations between behaviour and an aspect of anatomical masculinity (2D:4D) could emerge if anatomically more masculine men exhibit greater testosterone responses to an experimental intervention (which could affect subsequent behaviour). Moreover, McGlothlin *et al.* (2008) have recently shown that, in dark-eyed juncos (*Junco hyemalis*), testosterone increases in response to a GnRH challenge are positively associated with the size of a secondary sexual characteristic (a plumage ornament 'tail white'). However, the present study is the first demonstration that an index of anatomical masculinity (in this case, facial structure) is positively associated with directly measured testosterone responses to an experimental intervention in humans. Furthermore, facial structure is known to have a significant influence on mate preferences, whereas, to our knowledge, this has not been demonstrated directly for 2D:4D. If digit masculinity, such as facial masculinity, is associated with the size of testosterone responses to experimental interventions, then this could explain the findings that men with masculine 2D:4D exhibit greater responses to arousing stimuli (e.g. Van den Bergh & Dewitte 2006; Millet & Dewitte

2007). Both these previous studies employed stimuli likely to provoke increases in circulating testosterone, but neither measured these responses directly. As noted above, there are some intriguing findings of individual differences between men in the magnitude of their testosterone responses to contests (e.g. Cohen *et al.* 1996; Edwards *et al.* 2005) and further research is needed to establish how these might relate to other phenotypic traits (e.g. 2D:4D). Evidence of whether women exhibit similar responses in anticipation of, and following participation in, competition is inconsistent (e.g. Bateup *et al.* 2002; Kivlighan *et al.* 2005). It would, however, be interesting to investigate whether women with more masculine facial features exhibit more male-typical endocrine responses to competitive situations.

The present study replicates previous findings that the outcome of non-physical contests (Mazur *et al.* 1992; McCaul *et al.* 1992) and vicarious experiences of winning (Bernhardt *et al.* 1998) can affect testosterone levels in men. Individual differences in the magnitude of

these responses have been observed previously (Cohen *et al.* 1996; Edwards *et al.* 2005) and the present findings indicate that these are related to degree of facial anatomical masculinization. Further research is needed to establish whether individual differences in testosterone responsiveness are stable over time, and how men who show larger testosterone increases after success in competition respond to failure. Individual differences in the magnitude of testosterone responses to competitive stimuli could reflect either genetic differences or facultative adjustments in life-history strategy in response to early experiences, or both. Work in non-human species has indicated that testosterone may have a role in mediating life-history trade-offs between reproductive and immune functions (Muehlenbein & Bribiescas 2005). Underlying ability to cope with the costs associated with elevated testosterone (e.g. immunocompetence) may permit the development of a more competitive life-history strategy associated with larger testosterone responses to competitive stimuli and the development of more masculine facial features. It seems unlikely, however, that social events in themselves could drive facial masculinization independent of the characteristics of an individual male. In nonexperimental situations, competition outcomes are not randomly allocated. Consequently, the extent to which a particular male is exposed to the testosterone responses associated with success in competitive situations depends on the extent to which he is successful. Therefore, the association we report here supports the possibility that men's facial structure could signal the adoption of a more competitive life-history strategy and perhaps even predict success in competition.

An alternative interpretation of these findings is that facial masculinity is systematically related to the salience of success in competition for participants. There is evidence that testosterone responses depend on a man experiencing mood elevation as a consequence of winning (McCaul *et al.* 1992) and degree of mood elevation may depend on the salience of the competitive encounter for the individual, and the extent to which they attribute their success to internal, rather than external causes. For example, Gonzalez-Bono *et al.* (1999) studied professional basketball players, and found that post-game testosterone levels in winners were negatively associated with the extent to which individuals attributed victory to external causes (e.g. luck and referee's decisions). Similarly, Edwards *et al.* (2005) found that the percentage increase in testosterone seen after participation in a soccer match (and winning) was positively associated with self- and other-rated connectedness with teammates. It is possible that, perhaps as a consequence of experiencing more success in social competition outside the laboratory, men with more masculine facial structure were more likely to attribute their success in the experimental task used here to internal causes (e.g. skill, knowledge, ability) and this proximate psychological mechanism led to greater increases in posttask testosterone.

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## REFERENCES

- Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Angele, M. K., Schwacha, M. G., Ayala, A. & Chaudry, I. H. 2000 Effect of gender and sex hormones on immune responses following shock. *Shock* 14, 81-90.
- Archer, J. 2006 Testosterone and human aggression: an evaluation of the challenge hypothesis. *Neurosci. Biobehav. Rev.* 30, 319-345. (doi:10.1016/j.neubiorev.2004.12.007)
- Avignon, A., Radauceanu, A. & Monnier, L. 1997 Nonfasting plasma glucose is a better marker of diabetic control than fasting plasma glucose in type 2 diabetes. *Diabetes Care* 20, 1822-1826. (doi:10.2337/diacare.20.12.1822)
- Bateup, H. S., Booth, A., Shirtcliff, E. A. & Granger, D. A. 2002 Testosterone, cortisol, and women's competition. *Evol. Hum. Behav.* 23, 181-192. (doi:10.1016/S10905138(01)00100-3)
- Bernhardt, P. C., Dabbs Jr, J. M., Fielden, J. & Lutter, C. 1998 Changes in testosterone levels during vicarious experiences of winning and losing among fans at sporting events. *Physiol. Behav.* 65, 59-62. (doi:10.1016/S00319384(98)00147-4)
- Booth, A., Shelley, G., Mazur, A., Tharp, G. & Kittok, R. 1989 Testosterone, and winning and losing in human competition. *Horm. Behav.* 23, 556-571. (doi:10.1016/0018-506X(89)90042-1)
- Burriss, R. P., Little, A. C. & Nelson, E. 2007 2D: 4D and sexually dimorphic facial characteristics. *Arch. Sex. Behav.* 36, 377-384. (doi:10.1007/s10508-006-9136-1)
- Ceriello, A. 2000 The post-prandial state and cardiovascular disease: relevance to diabetes mellitus. *Diabetes Metab. Res. Rev.* 16, 125-132. (doi:10.1002/(SICI)1520-7560(200003/04)16:2 < 125::AID-DMRR90 > 3.0.CO;2-4)
- Cohen, D., Nisbett, R. E., Bowdle, B. F. & Schwarz, N. 1996 Insult, aggression, and the southern culture of honor: an 'experimental ethnography'. 1. *Pers. Soc. Psychol.* 70, 945-959. (doi:10.1037/0022-3514.70.5.945)
- Coutinho, M., Gerstein, H., Wang, Y. & Yusuf, S. 1999 The relationship between glucose and incident cardiovascular events. A metaregression analysis of published data from 20 studies of 95, 783 individuals followed for 12.4 years. *Diabetes Care* 22, 233-240. (doi:10.2337/diacare.22.2.233)
- Dabbs Jr, J. M. 1990 Salivary testosterone measurements: reliability across hours, days, and weeks. *Physiol. Behav.* 48, 83-86. (doi:10.1016/0031-9384(90)90265-6) DeBruine, L. M. et al. 2006 Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proc. R. Soc. B* 273, 1355-1360. (doi:10.1098/rspb.2005.3445)
- DECODE Study Group on behalf of the European Diabetes Epidemiology Study Group 1999 Glucose tolerance and mortality: comparison of WHO and American Diabetes Association diagnostic criteria. *Lancet* 354, 617-621. (doi:10.1016/S0140-6736(98) 12131-1)
- Donahue, R. P., Abbott, R. D., Reed, D. M. & Yano, K. 1987 Post-challenge glucose concentration and coronary heart disease in men of Japanese ancestry. Honolulu Heart Programme. *Diabetes* 36, 689-692. (doi:10.2337/diabetes.36.6.689)
- Edwards, D. A., Wetzel, K. & Wyner, D. R. 2005 Intercollegiate soccer: saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. *Physiol. Behav.* 87, 135-143. (doi:10.1016/j.physbeh.2005.09.007)

- Folstad, I. & Karter, A. J. 1992 Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139, 603-622. (doi:10.1086/285346)
- Gangestad, S. W. & Simpson, J. A. 2000 The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain. Sci.* 23, 573-644. (doi:10.1017/S0140525 X0000337X)
- Gladue, B., Boechler, M. & McCaul, K. 1989 Hormonal response to competition in human males. *Aggressive Behav.* 15, 409-422. (doi:10.1002/1098-2337(1989)15:6<409::AID-AB2480150602>3.0.CO;2-P)
- Gonzalez-Bono, E., Salvador, A., Serrano, M. A. & Ricarte, J. 1999 Testosterone, cortisol, and mood in a sports team competition. *Horm. Behav.* 35, 55-62. (doi:10.1006/hbeh.1998.1496)
- Hellhammer, D. H., Hubert, W. & Schurmeyer, T. 1985 Changes in saliva testosterone after psychological stimulation in men. *Psychoneuroendocrinology* 10, 77-81. (doi:10.1016/0306-4530(85)90041-1)
- Honekopp, J., Bartholdt, L., Beierb, L. & Liebert, A. 2007 Second to fourth digit length ratio (2D : 4D) and adult sex hormone levels: new data and a meta-analytic review. *Psychoneuroendocrinology* 32, 313-321. (doi:10.1016/j.psyneuen.2007.01.007)
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001 Male facial attractiveness: evidence for hormone mediated adaptive design. *Evol. Hum. Behav.* 22, 251-267. (doi:10.1016/S1090-5138(01)00066-6)
- Jones, B. C., Little, A. C., Boothroyd, L. G., DeBruine, L. M., Feinberg, D. R., Law Smith, M. J., Cornwell, R. E., Moore, F. R. & Perrett, D. I. 2005 Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm. Behav.* 48, 283-290. (doi:10.1016/j.yhbeh.2005.03.010)
- Kivlighan, K. T., Granger, D. A., Schwartz, E. B., Nelson, V. & Curran, M. 2004 Quantifying blood leakage into the oral mucosa and its effects on the measurement of cortisol, dehydroepiandrosterone, and testosterone in saliva. *Horm. Behav.* 46, 39-46. (doi:10.1016/j.yhbeh.2004.01.006)
- Kivlighan, K. T., Granger, D. A. & Booth, A. 2005 Gender differences in testosterone and cortisol response to competition. *Psychoneuroendocrinology* 30, 58-71. (doi:10.1016/j.psyneuen.2004.05.009)
- Little, A. C., Burt, D. M., Penton-Voak, I. S. & Perrett, D. I. 2001 Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. B* 268, 39--44. (doi:10.1098/rspb.2000.1327)
- Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. 2002 Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc. R. Soc. B* 269, 1095-1100. (doi:10.1098/rspb.2002.1984)
- Little, A. C., Cohen, D. L., Jones, B. C. & Belsky, J. 2007 Human preferences for facial masculinity change with relationship type and environmental harshness. *Behav. Ecol. Sociobiol.* 61, 967-973. (doi:10.1007/s00265-006-0325-7)
- Manning, J. T. 2002 *Digit ratio: a pointer to fertility, behaviour and health*. New Brunswick, NJ: Rutgers University Press.
- Manning, J. T. *et al.* 2000 The 2nd:4th digit ratio, sexual dimorphism, population differences

- and reproductive success: evidence for sexually antagonistic genes? *Evol. Hum. Behav.* 21, 163-183. (doi:10.1016/S1090-5138(00)00029-5)
- Mazur, A. & Lamb, T. 1990 Testosterone, status, and mood in human males. *Horm. Behav.* 14, 236-246. (doi:10.1016/00 18-506X(80)90032-X)
- Mazur, A., Booth, A. & Dabbs, J. M. 1992 Testosterone and chess competition. *Soc. Psychol. Q.* 55, 70-77. (doi:10.2307/2786687)
- Mazur, A., Susman, E. J. & Edelman, S. 1997 Sex difference in testosterone response to a video game contest. *Evol. Hum. Behav.* 18, 317-326. (doi:10.1016/S10905138(97)00013-5)
- McCaul, K. D., Gladue, B. A. & Joppa, M. 1992 Winning, losing, mood, and testosterone. *Horm. Behav.* 26, 486-504. (doi:10.1016/00 18-506X(92)90016-0)
- McGlothlin, J. W., Jawor, J. M., Greives, T. J., Casto, J. M., Phillips, J. L. & Ketterson, E. D. 2008 Hormones and honest signals: males with larger ornaments elevate testosterone more when challenged. *J. Evol. Biol.* 21, 39-48. (doi:10.1111/j.1420-9101.2007.01471.x)
- Messingham, K. A. N., Shirazi, M., Duffner, L. A., Emanuele, M. A. & Kovacs, E. J. 2001 Testosterone receptor blockade restores cellular immunity in male mice after burn injury. 1. *Endocrinol.* 169, 299-308. (doi:10.1677/joe.0.1690299)
- Millet, K. & Dewitte, S. 2007 Digit ratio (2D : 4D) moderates the impact of an aggressive music video on aggression. *Pers. Individ. Diff.* 43, 289-294. (doi:10.1016/j.paid.2006.11.024)
- Muehlenbein, M. P. & Bribiescas, R. G. 2005 Testosterone-mediated immune functions and male life histories. *Am. J. Hum. Biol.* 17, 527-558. (doi:10.1002/ajhb.20419)
- 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)
- 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. 2000 Female preference for male faces changes cyclically: further evidence. *Evol. Hum. Behav.* 21, 39-48. (doi:10.1016/S1090-5138(99)00033-1)
- Penton-Voak, I. S. & Perrett, D. I. 2001 Male facial attractiveness: perceived personality and shifting female preferences for male traits across the menstrual cycle. *Adv. Stud. Behav.* 30, 219-259. (doi:10.1016/S00653454(01)80008-5)
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Menstrual cycle alters face preference. *Nature* 399, 741-742. (doi:10.1038/21557)
- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M. & Perrett, D. I. 2001 Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proc. R. Soc. B* 268, 1617-1625. (doi:10.1098/rspb.2001.1703)
- Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P. & Perrett, D. I. 2003 Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). 1. *Comp. Psychol.* 117, 264-271. (doi:10.1037/0735-7036.117.3.264)
- Rhodes, G. 2006 The evolutionary psychology of facial beauty. *Annu. Rev. Psychol.* 57, 199-226. (doi:10.1146/annurev.psych.57.102904.190208)
- Roberts, M. L., Buchanan, K. L. & Evans, M. R. 2004 Testing the immunocompetence

- handicap hypothesis: a review of the evidence. *Anim. Behav.* 68, 227-239. (doi:10.1016/j.anbehav.2004.05.001)
- Roney, J. R. & Simmons, Z. L. 2008 Women's estradiol predicts preference for facial cues of men's testosterone. *Horm. Behav.* 53, 14-19. (doi:10.1016/j.yhbeh.2007.09.008)
- Roney, J. R., Mahler, S. V. & Maestripieri, D. 2003 Behavioral and hormonal responses of men to brief interactions with women. *Evol. Hum. Behav.* 24, 365-375. (doi:10.1016/S1090-5138(03)00053-9)
- Roney, J. R., Hanson, K. N., Durante, K. M. & Maestripieri, D. 2006 Reading men's faces: women's mate attractiveness judgments track men's testosterone and interest in infants. *Proc. R. Soc. B* 273, 2169-2175. (doi:10.1098/rspb.2006.3569)
- Roney, J. R., Lukaszewski, A. W & Simmons, Z. L. 2007 Rapid endocrine responses of young men to social interactions with young women. *Horm. Behav.* 52, 326-333. (doi:10.1016/j.yhbeh.2007.05.008)
- Stratton, I., Adler, A., Neil, H. A., Matthews, D., Manley, S., Cull, C., Hadden, D., Turner, R. & Holman, R. 2000 Association of glycaemia with macrovascular and microvascular complications of type 2 diabetes (UKPDS 35): prospective observational study. *Br. Med. J.* 321, 405-412. (doi:10.1136/bmj.321.7258.405)
- Van den Bergh, B. & Dewitte, S. 2006 Digit ratio (2D: 4D) moderates the impact of sexual cues on men's decisions in ultimatum games. *Proc. R. Soc. B* 273, 2091-2095. (doi:10.1098/rspb.2006.3550)
- 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)
- Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., Feinberg, D. R., Sharp, M. & Al-Dujaili, E. A. S. 2007 Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Horm. Behav.* 52, 156-161. (doi:10.1016/j.yhbeh.2007.01.010)
- Welling, L. L. M., Jones, B. C. & DeBruine, L. M. 2008 Sex drive is positively associated with women's preferences for sexual dimorphism in men's and women's faces. *Pers. Individ. Diff.* 44, 161-170. (doi:10.1016/j.paid.2007.07.026)
- Wingfield, J. C., Hegner, R. E., Dufty Jr, A. M. & Ball, G. F. 1990 The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136, 829-846. (doi:10.1086/285134)