

Second to fourth digit ratio, testosterone and perceived male dominance

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Previous studies have shown that male faces with extreme features associated with testosterone are perceived as dominant and masculine. Women have been reported to prefer more masculinized male faces as they may consider testosterone markers to be an 'honest' indication of good health, and such considerations may underlie their aesthetic preferences. However, pronounced testosterone facial markers are also associated with dominance, and several negative personality traits. This suggests that female aesthetic preferences may be an adaptive compromise between positive attributes associated with higher than average testosterone, and negative attributes associated with more extreme masculinization. This current study attempts to clarify the role of hormone markers in female perceptions of dominance, masculinity and attractiveness, in male facial images. Recent evidence suggests that the relative length of the 2nd to 4th finger (2D: 4D ratio) is a pointer to prenatal testosterone levels and may thus serve as a window to the prenatal hormonal environment. We measured 2D: 4D in a sample of male college students and took salivary samples to analyse circulating levels of testosterone. Women rated facial images of these males for dominance, masculinity and attractiveness. Our results show that male 2D: 4D was significantly negatively related to perceived dominance and masculinity but not attractiveness. Circulating testosterone levels were not related to dominance, masculinity or attractiveness. These findings suggest that: (i) high prenatal levels of testosterone serve to 'organize' male facial features to subsequently reflect dominance and masculine characteristics presumably activated during puberty; and (ii) attractiveness is not directly related to testosterone levels. We conclude that facial dominance and masculinity reflect a male's perceived status rather than his physical attraction to women.

Keywords: finger length ratio; testosterone; dominance; masculinity

1. INTRODUCTION

The face plays a crucial role in animal and human social cognition and behaviour. Evidence from primates shows that certain brain structures specialize in perceiving facial expressions of emotions and intentions, and in regulating emotional and behavioural responses to these expressions (Morris *et al.* 1996). Human faces signal qualities that are stable over time, such as attractiveness as a potential mate (Grammer & Thornhill 1994; Barber 1995) or dominance (Zebrowitz & Montepare 1992; Collins & Zebrowitz 1995; Mueller & Mazur 1997). Although we assume that facial beauty conveys a wealth of information concerning an individual's mate value, the actual role of perceived facial dominance still remains equivocal.

Facial dominance may signal subjective intentions (Maynard-Smith & Harper 1988; Harper 1991) as well as an objective potential for action (Mazur & Booth 1998). Features that contribute to perceived facial dominance, such as strong jaws or broad cheek bones (see, for example, Cunningham *et al.* 1990), may indicate superior physical strength. Several authors have suggested that such features may relate to circulating testosterone levels (Grammer & Thornhill 1994; Thornhill & Gangestad

As Mazur & Booth (1998) pointed out, early exposure to higher levels of testosterone are likely to produce more male-like characteristics (masculinization) and fewer female characteristics (defeminization) whereas less exposure to testosterone causes the reverse. These preand perinatal hormone effects are regarded as organizing the architecture of the body and brain. When male testosterone increases later in life during puberty, it is thought to activate pre-existing structures; for example, in males higher androgen serum levels at puberty together with a higher androgen receptor expression at certain skeletal sites, may contribute to sex differences in facial morphology (Kasperk et al. 1997). In males, a high testosterone-to-oestrogen ratio facilitates the lateral growth of the cheekbones, mandibles and chin, the forward growth of the bones of the eyebrow ridges, and the lengthening of the lower facial bone, all of which are considered masculine facial features (Thornhill & Gangestad 1999; Fink & Penton-Voak 2002; Grammer et al. 2003). Oestrogen inhibits this growth, leading to a feminized facial shape with high eyebrows, more gracile jaw and fuller lips. A preference for sex-typical traits may operate in females' judgements of male facial attractiveness, and males' preferences for female faces. Whereas some studies support the hypothesis that women prefer masculinized male faces, other studies indicate that women do not have clear

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^{1996),} further suggesting a link to dominance behaviour (Mazur & Booth 1998).

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preferences for such traits in males. Perrett *et al.* (1998) showed that females' preferences for male faces were apparently driven by stereotypical personality attributions: highly masculinized male faces were perceived as less warm, less honest and more dominant than feminized male faces. Such attributions may have a kernel of truth, as high testosterone has been linked with anti-social behaviour in men (Dabbs *et al.* 1991).

In mammals, the growth of secondary sexual traits is linked to levels of androgens (Owens & Short 1995), which depress immune system function (Folstad & Karter 1992). Evolutionary theory suggests that only males in good condition can bear the 'handicap' of large secondary sexual traits that represent an honest advertisement of male viability. As signalling facial dominance is therefore costly, it is assumed that dominant looks may signal high status. Across a wide variety of species, behaviours intended to achieve, maintain and enhance status are observed primarily among high-testosterone individuals (Kraus et al. 1999; Josephs et al. 2003). If perceived facial dominance does indeed relate to a potential for high status in male dominance hierarchies, then in the human resource-based mating system (Buss 1989; Kenrick & Keefe 1992), it may signal a fitness relevant quality (Dewsbury 1982; Mueller 1993; Ellis 1995).

It is particularly important for humans to distinguish between dominant behaviour, which aims at achieving and maintaining high status and greater control of resources over a conspecific, and aggressive behaviour, which aims at inflicting physical injury on a conspecific. In this paper, we only discuss the former. While the relationship between testosterone levels and human aggression remains equivocal (Archer 1991), Mazur & Booth (1998) concluded that high levels of testosterone were linked with dominance and competitiveness in human males; specifically, they suggested that testosterone rises in the face of a challenge and activates behaviours intended to dominate and enhance status.

In support, several studies have reported links between testosterone and human dominance encounters (Booth et al. 1989; Schaal et al. 1996; Salvador et al. 1999; Dabbs et al. 2001; Neave & Wolfson 2003). However, some researchers have criticized the simplicity of this theory (see author comments following Mazur & Booth 1998), and have pointed out the problems in attempting to link a single hormonal measure to certain behaviours (Brain 1998). Furthermore, Campbell et al. (1998) noted that as dominant/aggressive behaviour emerges early in childhood, the major impact of testosterone may be acting at an organizational rather than an activational level.

Until recently, ascertaining foetal exposure to testosterone has been difficult. However, Manning (2002) has recently summarized the evidence that testosterone stimulates prenatal growth of the 4th finger while oestrogen promotes the growth of the 2nd finger. A low 2D: 4D ratio (4th finger longer than the second) may thus act as a marker for a uterine environment high in testosterone and low in oestrogen, and such a ratio is most often seen in males. Conversely, a high 2D: 4D ratio may serve as a marker for a uterine environment low in testosterone and high in oestrogen, and is most often found in females. In support, (i) 2D: 4D ratio demonstrates a sexually dimorphic pattern that appears to be established at a very early

age and is correlated with testosterone concentrations (Manning et al. 1998; Ronalds et al. 2002); (ii) a low 2D: 4D ratio is associated with male-typical attributes such as better spatial ability (Manning & Taylor 2001), left-handedness (Manning et al. 2000) and a predisposition towards autism (Manning et al. 2001); (iii) the waist: hip ratio of mothers, a positive correlate of testosterone, is negatively associated with the 2D: 4D ratio of their children (Manning et al. 1999); and (iv) children with congenital adrenal hyperplasia, a genetic disorder associated with high prenatal androgens, have lower 2D: 4D ratios than normal controls (Brown et al. 2002).

As testosterone is strongly implicated in establishing the sexually dimorphic 2D: 4D ratio, and as this hormone has also been linked with male dominance behaviours, Manning (2002) proposed that a low 2D: 4D ratio may be associated with assertiveness and dominance but as yet, this possible link remains speculative. In the current paper we aimed to establish whether organizational levels of testosterone (as measured by 2D: 4D ratio) are related to activational levels of testosterone, and perceived facial 'dominance', and 'masculinity'. We predicted that males with low 2D: 4D (i.e. high prenatal levels of testosterone) would be rated by females as being higher in dominance and masculinity.

In addition, although some evidence demonstrates a female preference for exaggerated male facial characteristics (e.g. Scheib et al. 1999) the relationship between facial dominance and attractiveness remains unclear. Swaddle & Reierson (2002) recently showed that high testosterone faces reveal dominance. However, they did not find evidence of directional selection for increased (or decreased) testosterone in terms of male facial attractiveness. Consequently, these authors argued that this reflects stabilizing selection acting on testosterone through mate preferences. We therefore aimed to investigate the possible relationship between male 2D: 4D ratio and facial attractiveness judgements made by females. We predicted that if women consider dominant and masculine faces as attractive, then-in addition to dominance and masculinity-2D:4D should also be negatively related to male perceived attractiveness.

Finally, to identify possible links between activational levels of testosterone and female perceptions of male dominance, masculinity and attractiveness, we also took salivary samples of free testosterone from the male volunteers.

2. MATERIAL AND METHODS

(a) Participants

We recruited 48 male participants from undergraduate courses at Northumbria University. The mean age of the sample was 21.3 years (range of 18–33 years, s.d. = 3.4). All claimed to be heterosexual and right-handed.

(b) Procedure

(i) Data recording

Participants gave their informed written consent in accordance with Northumbria University School of Psychology and Sport Sciences Ethics Committee guidelines. Age, body height and weight were recorded.

We measured the lengths of the 2nd and 4th digits of the left and right hands from the tip of the finger to the ventral proximal crease from photocopies. Where there was a band of creases at the base of the digit, we measured from the most proximal of these. For 16 right and left hands, the 2nd and 4th digits were also measured directly from the hand and from the photocopies to establish repeatabilities. All measurements were made with digital Vernier callipers measuring to 0.01 mm.

Colour digital images of each participant's face were taken at high resolution under standardized light conditions in frontal view. Participants were advised to remove any facial adornment, look directly into the camera and present a neutral facial expression.

Finally, male participants provided a salivary sample from which circulating levels of free testosterone could be measured. They were given labelled, lidded cups and sugarless chewing gum, and were asked to chew the gum and deposit enough saliva to fill the bottom of the cup (5 ml) the samples were then frozen to $-20~\rm ^{\circ}C$ before analysis.

(ii) Face ratings

To obtain independent ratings of perceived male facial dominance, masculinity and attractiveness, 36 female raters from a different local university, mean age of 22.1 years (range of 19–30 years, s.d. = 2.7) rated each face. Faces were randomly presented by computer, and remained on screen until raters provided a measure of perceived dominance, masculinity, and attractiveness using a 7-point scale (1 = extremely subordinate/feminine/unattractive, 7 = extremely dominant/masculine/attractive). At the end of the session, female raters were asked if they recognized any of the faces they had seen (none did).

(c) Hormone analyses

Salivary testosterone was used as it is less stressful and invasive than serum sampling, and causes minimal disruption to normal routines (Ellison 1988). A strong correlation has been reported between salivary and serum testosterone levels (Vittek et al. 1985). As circadian and circannual changes in testosterone have been reported (Nieschlag 1974; Dabbs 1990) samples were collected at the same time of day (between 10.00 and 15.00) within a period of two weeks (in November).

Testosterone levels in saliva samples were measured by using a modified serum radioimmunoassay. Before assaying, the previously frozen samples were thawed and centrifuged. The assay used the Coat-A-Count total testosterone kit (Euro/DPC, UK), which is a solid phase radioimmunoassay, based on testosteronespecific antibodies immobilized to the wall of a polypropylene tube. 125I-labelled testosterone competes for a fixed time with testosterone in the saliva sample for antibody sites. The tube is then decanted, to separate antibody-bound testosterone (on walls of the tube) from free testosterone (in the decanted solution). The tubes are counted using a gamma counter and the amount of testosterone present in the saliva sample is determined from a calibration graph of known standards, where higher gamma counts equate to lower testosterone levels. This procedure has to be modified to allow for measurement of the lower hormone concentrations in saliva by diluting the supplied Coat-A-Count testosterone standards 20-fold and extending the incubation time from 3 h at 37 °C to 24 h at room temperature. Each sample was assayed in duplicate and the mean value for the two duplicates taken as the value for each sample. The tubes were each counted for one minute using a Packard Cobra II gamma counter.

Table 1. Correlation of hormonal variables with perceived measures.

(LH, left hand; RH, right hand; T, testosterone.)

	LH 2D : 4D	RH 2D: 4D	Т
age height dominance masculinity attractiveness testosterone	0.111 -0.085 -0.306* -0.309* -0.231 0.034	-0.071 0.040 $-0.278*$ $-0.305*$ -0.064 -0.052	-0.298* -0.198 0.086 0.076 -0.017

^{*} p < 0.05.

3. RESULTS

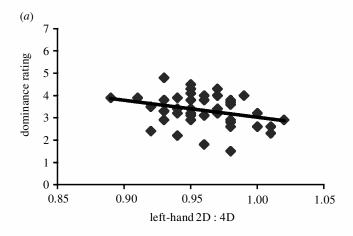
In the right hand the first and second measures of 2D: 4D from photocopies had a high intraclass correlation coefficient ($r_1 = 0.96$), as did the mean of these two measures compared to right 2D:4D calculated from measurements directly on the fingers $(r_1=0.91)$. Repeated measures ANOVA analyses showed that measurement error was low in relation to real differences in 2D:4D ratio between individuals (2D:4D from photocopies F = 49.37, p = 0.0001; 2D: 4D from photocopies and direct from fingers F = 21.70, p = 0.0001). In the left hand the intraclass correlation between measures of 2D: 4D from photocopies was high $(r_1 = 0.94)$, but from a comparison of photocopied and direct-measured 2D: 4D it was quite low $(r_1 = 0.67)$. However, repeated measures ANOVA analyses showed that both intraclass correlation coefficients were significant (2D:4D from photocopies F = 31.52, p = 0.0001; 2D: 4D from photocopies and direct from fingers F = 5.10, p = 0.009). We concluded that our measures of 2D: 4D from photocopies of the hands reflected real differences between individuals in the study.

Pearson correlations were calculated analysing the relationships between digit ratios, perceived dominance, masculinity, and attractiveness ratings, and salivary testosterone. Values of p equal to or less than 0.05, in one-tailed tests were considered significant. Correlations are shown in table 1.

As age and body height may influence certain physiological variables as well as anatomical traits we firstly correlated these factors with the 2D: 4D ratio. Neither were associated with the 2D: 4D ratio, but age was associated with attractiveness ratings (r = -0.265, p = 0.034)—the older the participant the lower the rating, and salivary testosterone level (r = -0.298, p = 0.022)—the older the participant the lower the level (table 1). Left-hand and right-hand 2D: 4D ratios were strongly correlated with one another (r = 0.642, p = 0.000).

Both left-hand and right-hand 2D: 4D ratios were significantly negatively correlated with female ratings of perceived male dominance (r = -0.306, p = 0.017; r = -0.278, p = 0.028, respectively) indicating the lower the ratio, the higher the rating of male facial dominance (see figure 1).

Similarly, both left-hand and right-hand 2D: 4D ratios were significantly negatively correlated with female ratings of perceived masculinity (r = -0.309, p = 0.016; r = -0.305, p = 0.018, respectively) indicating the lower the



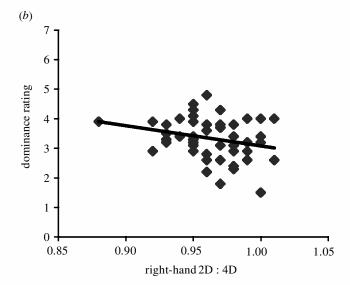


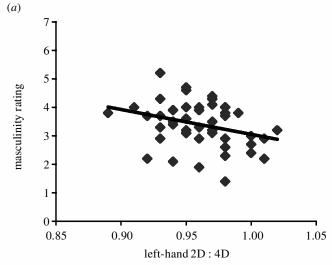
Figure 1. (a) Scatterplot of left-hand 2D: 4D ratio and female perceptions of male dominance. (b) Scatterplot of right-hand 2D: 4D ratio and female perceptions of male dominance.

ratio, the higher the rating of male facial dominance (see figure 2). In addition, attractiveness ratings did not significantly correlate with 2D:4D (left hand: r = -0.231, p = 0.057; right hand: r = -0.064, p = 0.333).

Neither left-hand and right-hand 2D: 4D ratios, nor face ratings of 'dominance', 'masculinity' and 'attractiveness' displayed significant correlations with salivary testosterone (table 1). Finally, attractiveness ratings were significantly positively correlated with both ratings of facial dominance (r = 0.462, p = 0.000) and masculinity (r = 0.428, p = 0.001).

4. DISCUSSION

The aim of this study was to ascertain possible relationships between organizational effects of testosterone (by 2D: 4D finger length ratio), activational levels of testosterone (via saliva) and perceived male facial characteristics. Manning (2002) suggested that a low 2D: 4D ratio may be associated with male assertiveness and dominance, and we find some support for this prediction. Our results showed that both left- and right-hand 2D: 4D ratios were significantly negatively correlated with female ratings of perceived male dominance and masculinity from colour



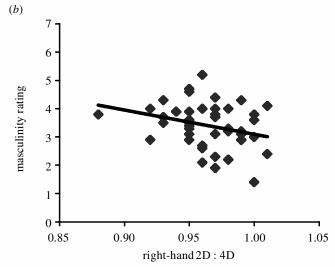


Figure 2. (a) Scatterplot of left-hand 2D: 4D ratio and female perceptions of masculinity. (b) Scatterplot of right-hand 2D: 4D ratio and female perceptions of masculinity.

photographs (figures 1 and 2). To clarify this, measurements made of male digit ratios were strongly related to female perceptions of these same participants from headonly colour photographs. This finding implies that high prenatal levels of testosterone (resulting in a low 2D: 4D ratio) serve to 'organize' male facial features (presumably activated during puberty) to subsequently reflect dominance/masculine characteristics. This is in accord with the assertion of Campbell *et al.* (1998) that human dominance behaviours may reflect organizational rather than activational processes.

The development of certain facial features that contribute to perceptions of dominance may be testosterone induced, and several authors have proposed that such 'honest' markers affect judgements of certain facial characteristics. For example, Swaddle & Reierson (2002) digitally manipulated male faces to mimic shape variations caused by varying levels of testosterone. Female raters selected the most dominant and attractive faces, with 'high-testosterone' faces producing higher dominance ratings (though lower attractiveness ratings). Dominant-looking males may be preferred as mates because their

looks are 'honest' indicators of their potential to achieve and maintain a high status (Mueller & Mazur 1997).

However, we found no evidence that circulating levels of testosterone in our male volunteers were associated with female ratings of their perceived dominance/masculinity, indeed, testosterone levels within the males were not related to their 2D: 4D ratios. This is perhaps not so surprising, if male facial characteristics are organized before birth and then sculpted during puberty, then we should not expect fluctuating levels to be related to perceived facial characteristics.

Our data revealed that perceived dominance and masculinity are both significantly correlated with attractiveness ratings, but this may not be simply taken as support for a direct link between these features. In the literature, several reports of an association between attractiveness and dominance exist (e.g. Keating 1985; Barber 1995), but we know that this also entails some neonate features such as large eyes, a small nose and a high forehead. Consequently, as Mueller & Mazur (1997) point out, a dominant-looking man may not be rated as attractive, and an attractive man need not be perceived as being dominant. Mueller & Mazur (1997) therefore propose that the effects of facial dominance and attractiveness should be considered separately by statistical analysis. Our data support this view of the 2D: 4D ratio as a pointer to prenatal (and actual) levels of testosterone correlated with perceived dominance and masculinity, but not with attractiveness. In addition, as we did not find a relationship between attractiveness and circulating levels of testosterone, we may speculate that any association between these features also operates at an early stage in life.

During early development, very high levels of testosterone are supposed to negatively affect development, resulting in the expression of bodily asymmetries. The 2D: 4D ratio has been suggested to serve as a pointer to the prenatal hormonal environment of a foetus. For our study, we may speculate that the association between attractiveness, dominance and masculinity on the basis of underlying hormones, namely testosterone, is based on the fact that: (i) the attractiveness-hormone link is a pointer to developmental stability and immunocompetence; and (ii) features developed under the influence of testosterone do not directly account for attractiveness but rather for male dominance and masculinity, both of which are features of perceived behavioural social status rather than mate value. The present findings are in accord with previous studies (Mueller & Mazur 1997; Mazur & Booth 1998) proposing that facial dominance is an honest signal of dominant behaviour. As it suggests, a male's mate value depends on his potential to achieve high status in social contexts.

REFERENCES

- Archer, J. 1991 The influence of testosterone on human aggression. Br. J. Psychol. 82, 1-28.
- Barber, N. 1995 The evolutionary psychology of physical attractiveness: sexual selection and human morphology. Ethol. Sociobiol. 16, 395-424.
- Booth, A., Shelley, G., Mazur, A., Tharp, G. & Kittok, R. 1989 Testosterone and winning and losing in human competition. Hormones Behav. 23, 556-571.

- Brain, P. F. 1998 Androgens and human behaviour: a complex relationship. Behav. Brain Sci. 21, 363-364.
- Brown, W. M., Hines, M., Fane, B. A. & Breedlove, S. M. 2002 Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. Hormones Behav. 42, 380-386.
- Buss, D. M. 1989 Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. Behav. Brain Sci. 12, 1-49.
- Campbell, A., Muncer, S. & Odber, J. 1998 Primacy of organising effects of testosterone. Behav. Brain Sci. 21, 365.
- Collins, M. & Zebrowitz, L. 1995 The contributions of appearance to occupational outcomes in civilian and military settings. J. Appl. Social Psychol. 25, 29-163.
- Cunningham, M. R., Barbee, A. P. & Pike, C. L. 1990 What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness J. Person. Social Psychol. 59, 61-72.
- Dabbs Jr, J. M. 1990 Age and seasonal variation in serum testosterone concentrations in men. Chronobiol. Int. 7, 245-249.
- Dabbs Jr, J. M., Jurkovic, G. & Frady, R. L. 1991 Salivary testosterone and cortisol among late adolescent male offenders. J. Abnormal Child Psychol. 19, 469-478.
- Dabbs Jr, J. M., Bernieri, F. J., Strong, R. K., Campo, R. & Milun, R. 2001 Going on stage: testosterone in greetings and meetings. J. Res. Person. 35, 27-40.
- Dewsbury, D. A. 1982 Domiance rank, copulatory behavior, and differential reproduction. Q. Rev. Biol. 57, 135-159.
- Ellis, L. 1995 Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethol. Sociobiol. 16, 257–333.
- Ellison, P. T. 1988 Human salivary steroids: methodological considerations and applications in physical anthropology. Yearbook Phys. Anthropol. 31, 115-142.
- Fink, B. & Penton-Voak, I. S. 2002 Evolutionary psychology of facial attractiveness. Curr. Direct. Psychol. Sci. 11, 154-158.
- Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. Am. Nat. 139, 603-622.
- Grammer, K. & Thornhill, R. 1994 Human facial attractiveness and sexual selection: the roles of averageness and symmetry. 7. Comp. Psychol. 108, 233-242.
- Grammer, K., Fink, B., Moller, A. P. & Thornhill, R. 2003 Darwinian aesthetics: sexual selection and the biology of beauty. Biol. Rev. 78, 385-407.
- Harper, D. G. C. 1991 Communication. In Behavioural ecology (ed. J. R. Krebs & N. B. Davies). Oxford: Blackwell Scien-
- Josephs, R. A., Newman, M. L., Brown, R. P. & Beer, J. M. 2003 Status, testosterone, and human intellectual performance: stereotype threat as status concern. Psychol. Sci. 14, 158-163.
- Kasperk, C., Helmboldt, A., Borcsok, I., Heuthe, S., Cloos, O., Niethard, F. & Ziegler, R. 1997 Skeletal site-dependent expression of the androgen receptor in human osteblastic cell populations. Calc. Tissue Int. 61, 464-473.
- Keating, C. 1985 Gender and the physiognomy of dominance and attractiveness. Social Psychol. Q. 48, 61-70.
- Kenrick, D. T. & Keefe, R. C. 1992 Age preferences in mates reflect sex differences in human reproductive strategies. Behav. Brain Sci. 15, 75-133.
- Kraus, C., Heistermann, M. & Kappeler, P. M. 1999 Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (Propithecus verreauxi). Physiol. Behav. 66, 855-861.
- Manning, J. T. 2002 Digit ratio: a pointer to fertility, behaviour, and health. New Brunswick, NJ: Rutgers University Press.

- Manning, J. T. & Taylor, R. P. 2001 2nd to 4th digit ratio and male ability in sport: implications for sexual selection in humans. *Evol. Hum. Behav.* 22, 61–69.
- Manning, J. T., Scutt, D., Wilson, J. & Lewis-Jones, D. I. 1998 The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Hum. Reprod.* 13, 3000–3004.
- Manning, J. T., Trivers, R. L., Singh, D. & Thornhill, R. 1999 The mystery of female beauty. *Nature* **399**, 214–215.
- Manning, J. T., Trivers, R. L., Thornhill, R. & Singh, D. 2000 The 2nd: 4th digit ratio and asymmetry of hand performance in Jamaican children. *Laterality* 5, 121–132.
- Manning, J. T., Baron-Cohen, S., Wheelwright, S. & Sanders, G. 2001 The 2nd to 4th digit ratio and autism. *Devl Med. Child Neurol.* 43, 160–164.
- Maynard-Smith, J. & Harper, D. G. C. 1988 The evolution of aggression: can selection create variability? *Phil. Trans. R. Soc. Lond.* B **319**, 557–570.
- Mazur, A. & Booth, A. 1998 Testosterone and dominance in men. *Behav. Brain Sci.* 21, 353–397.
- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J. & Dolan, R. J. 1996 A different neural response in the human amygdala in fearful and happy facial expressions. *Nature* 383, 812–815.
- Mueller, U. 1993 Social status and sex. Nature 363, 490.
- Mueller, U. & Mazur, A. 1997 Facial dominance in *Homo sapiens* as honest signalling of male quality. *Behav. Ecol.* 8, 569–579.
- Neave, N. & Wolfson, S. 2003 Testosterone, territorilaity, and the 'home advantage'. *Physiol. Behav.* 78, 269–275.
- Nieschlag, E. 1974 Circadian rhythms of plasma testosterone. In *Chronobiological aspects of endocrinology* (ed. J. Aschoff, F. Ceresa & F. Halberg), pp. 117–128. New York: Schattauer Verlag.

- Owens, I. P. F. & Short, R. V. 1995 Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. *Trends Ecol. Evol.* 10, 44–47.
- Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshi-kawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* 394, 884–887.
- Ronalds, G., Phillips, D. I., Godfrey, K. M. & Manning, J. T. 2002 The ratio of second to fourth digit lengths: a marker of impaired fetal growth? *Early Hum. Dev.* 68, 21–26.
- Salvador, A., Suay, F., Martinez-Sanchis, Simon, V. M. & Brain, P. F. 1999 Correlating testosterone and fighting in male participants. *Physiol. Behav.* 68, 205–209.
- Schaal, B., Tremblay, R. E., Soussignan, R. & Susman, E. J. 1996 Male testosterone linked to high social dominance but low physical aggression in early adolescence. J. Am. Acad. Child Adolescent Psychiat. 34, 1322–1330.
- Scheib, J., Gangestad, S. W. & Thornhill, R. 1999 Facial attractiveness, symmetry and cues of good genes. *Proc. R. Soc. Lond.* B 266, 1913–1917. (DOI 10.1098.rspb.1999.0866.)
- Swaddle, J. P. & Reierson, G. W. 2002 Testosterone increases perceived dominance but not attractiveness in human males. *Proc. R. Soc. Lond.* B 269, 2285–2289. (DOI 10.1098/rspb. 2002.2165.)
- Thornhill, R. & Gangestad, S.W. 1996 The evolution of human sexuality. *Trends Ecol. Evol.* 11, 98–102.
- Thornhill, R. & Gangestad, S.W. 1999 Facial attractiveness. Trends Cogn. Sci. 3, 452–460.
- Vittek, J., L'Hommedieu, D. G., Gordon, G. G., Rappaport, S. C. & Southren, A. L. 1985 Direct radioimmunoassay (RIA) of salivary testosterone: correlation with free and total serum testosterone. *Life Sci.* 37, 711–716.
- Zebrowitz, L. A. & Montepare, J. 1992 Impressions of baby-faceness and attractiveness across the life span. *Devl Psychol.* 28, 1143–1152.