Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces

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The stress-linked immunocompetence handicap hypothesis (SL-ICHH) of sexual selection incorporates a role of the stress hormone corticosterone (C; cortisol in humans) in relationships between testosterone (T), immunity and secondary sexual trait expression. In support of this, C has been shown to mediate and moderate relationships between T and immune response and to be inversely related to attractiveness in some avian species. We predicted that female preferences for cues to T in human male faces would be contingent upon co-occurring cortisol levels. In study 1, we tested relationships between T and cortisol and attractiveness, masculinity and health ratings of raw male faces. We found cortisol to be inversely related to attractiveness. In study 2, we tested female preferences for male faces that were parametrically manipulated on the basis of cues to naturally co-occurring levels of T and cortisol across the menstrual cycle. Women preferred cues to low cortisol in general and in the fertile phase of the cycle, and there was an interaction between T and cortisol in general and in the non-fertile phase. Results were consistent with the SL-ICHH but not the original immunocompetence handicap model: females expressed preferences for cues to cortisol but not for cues to T, except in interaction with the stress hormone. Results inform the SL-ICHH by demonstrating female preferences for low cortisol and the nature of its interaction with T in humans, as well as indicating the traits that may be signalled by different combinations of the hormones including immune response, current health and resource acquisition characteristics.

Keywords: stress-linked immunocompetence handicap hypothesis; faces; attractiveness; cortisol; testosterone

1. INTRODUCTION

In the immunocompetence handicap hypothesis (ICHH), females prefer exaggerated male secondary sexual traits that provide an honest cue to heritable immunocompetence [1]. In this model, testosterone (T) is a mediator of the relationship between immunocompetence and signal intensity owing to its role in secondary sexual trait development and immunosuppressive action. Males with a weak immune response are unable to afford full trait expression owing to the associated costs of elevated T. Degree of masculinization of the human male face correlates with circulating T levels [2–4], and so may provide an honest indicator of heritable immunity to infection (e.g. [5,6]). In support of this, masculinity is associated with long-term health [7,8] and genetic profiles associated with immunity ([9], but see [10]). There are systematic differences between women and contexts that result in a lack of consistency in preferences for masculine-faced males (e.g. [11,12]). Female preferences for masculinized faces, for example, are strongest during the fertile phase

of the menstrual cycle (e.g. [13–16]). This may reflect a trade-off in female preferences, in which women prefer cues to heritable immunity during times of high conception risk but favourable personality characteristics associated with feminine faces at other times [5,6,13,15,17].

Recently, inconsistencies in support for the ICHH have received attention. While a number of studies have demonstrated an immunosuppressive effect of T in avian species (e.g. [18–20]) others have failed to do so (e.g. [21,22]). A meta-analysis of experimental manipulations of T demonstrated strong support for the ICHH only for levels of ecto-parasites in reptiles [23]. The authors interpreted these inconsistencies in the context of the stress-linked ICHH (SL-ICHH), proposed by Møller [24] and Evans *et al.* [25], in which the effects of T on the immune system occur indirectly, through covariance with the stress hormone corticosterone (C). C is released via the hypothalamic-pituitary-adrenal axis and moderates the body's response to long-term stress (e.g. [26,27]). Glucocorticoids are involved in moderation of the immune response (e.g. [28]) and chronically elevated levels suppress reproductive function (e.g. [29,30]). Evans *et al.* [25] demonstrated that experimentally elevated T

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enhanced immune response in the house sparrow (*Passer domesticus*), once C was controlled for statistically, providing support for the SL-ICHH and argued that T may both suppress and enhance the immune response under certain circumstances. While there is further evidence for a role of C in the relationship between T and immune response, it has failed to support the mechanism proposed by the SL-ICHH. Both hormones, for example, enhanced an antibody response when levels of the other were high in the zebra finch (*Taeniopygia guttata*; [31]), but neither influenced immune function in a similar study of Japanese quail (*Coturnix japonica*; [32]), suggesting that the mechanism by which the two hormones interact to influence immune response is more complicated than simple covariance across species. One study has explored female preferences for cues to T and C, in which female zebra finches were shown to prefer males selected for low peak and current C levels while exhibiting no preference for T, behaviour or body mass [33]. The patterns of relationships between T, C, immune response and trait expression, then, are complex and have been argued to represent adaptive responses to species-specific life histories and ecologies [34]. Investigation of these relationships across species and contexts is required to determine the ways in which stress hormones influence immune response and trait expression in order to develop a more powerful model of hormonally mediated sexual selection.

The aim of the current research was to test the effects of T and C, independently and in combination with one another, on the attractiveness of human male faces. In humans, both T (e.g. [35–37]) and C (cortisol; e.g. [38]) can suppress the immune system and peak levels covary (e.g. after exercise; [39]). Human faces provide a valuable opportunity to explore the mechanisms of the SL-ICHH as it is possible to obtain detailed measures of female preferences for stimuli experimentally manipulated on the basis of naturally co-occurring levels of the hormones. Predictions derived from the ICHH were that there will be a positive relationship between women's attractiveness judgements and cues to T in male faces during the fertile phase of the menstrual cycle. Predictions derived from the SL-ICHH were that attractiveness judgements will also be influenced by levels of C. We measured baseline levels of T and C as the SL-ICHH refers to these [25]. In study 1, relationships between ratings of attractiveness, health and masculinity and levels of C and T were explored in raw male faces. In study 2, composite male faces that differed in cues to levels of C and T were rated for attractiveness across the menstrual cycle.

2. STUDY 1

(a) Introduction

We explored relationships between circulating T and C and the attractiveness, masculinity and health of male faces to determine whether (i) T or C predicted the attractiveness, masculinity or health of the face and (ii) whether T or C mediated or moderated the effects of the other on ratings of attractiveness, masculinity or health.

(b) Methods

(i) Facial stimuli

Sixty-nine male students, in good health, were recruited from the University of St Andrews (mean age: 20.49, s.d.: 1.63).

Participants provided saliva samples during both a morning and an afternoon session (sessions were not separated by more than 24 h) by chewing a quarter stick of sugar-free gum to stimulate salivary flow, and depositing 3–5 ml of saliva. Samples were frozen at -20°C until analysis at Queen Margaret University Immunoassay Laboratories using an in-house enzyme-linked immunosorbent assay [40]. The assay procedure used the indirect, competitive binding technique in which samples were first extracted using diethyl ether, 4 ml of ether added to 500 μl of sample, vortexed for 10 min then frozen at -80°C until the aqueous phase was frozen. The unfrozen ether was then decanted and evaporated with forced nitrogen and samples reconstituted with 500 μl of assay buffer and vortex mixed prior to assay. Assay sensitivity was 1.5 pg ml^{-1} ; intra- and inter-assay coefficients, obtained over 50 assay runs, were 2.7 per cent and 6.8 per cent, respectively; cross reactivity with related compounds was minimal and the standard curve was highly reproducible ($r = 0.998$). Salivary C levels were determined using the same indirect assay procedure. Cross reactivity with cortisone was 1.2 per cent, C 1.4 per cent, Deoxycortisol 1 per cent, T 0.4 per cent and other steroids less than 0.001 per cent. Intra- and inter-assay precision values were 3.2 per cent and 5.7 per cent, respectively. The assay also involved an extraction step and recovery studies for a range of C levels from 2.6 to 4.08 ng ml^{-1} were 91.8–106.7%. Assay sensitivity was 0.12 n mol l^{-1} . Hormonal analysis was successful for 51 participants (i.e. samples were not contaminated) and all had hormones within normal ranges. Mean levels of each hormone were calculated for each participant. T ranged from 0.07 to 0.63 ng ml^{-1} (mean: 0.3, s.d.: 0.11) and C from 3.7 to 24.04 nmol l^{-1} (mean: 10.88, s.d.: 5.4). During one of the testing sessions (i.e. morning or evening), participants were photographed under standardized diffuse flash lighting. Data from 12 participants were excluded owing to facial hair or spectacles in photographs.

(c) Ratings

(i) Participants

Forty-two heterosexual female participants (mean age: 20.14, s.d.: 2.89) were recruited from the University of Abertay Dundee.

(ii) Procedure

Participants indicated their age and sexual orientation. The 39 male faces were then displayed in random order on a computer screen and participants were asked to rate them for attractiveness, masculinity and health on 1–7 likert scales (1 = not at all, 7 = extremely).

(d) Results

Multiple regression models were constructed to investigate relationships between T and C and attractiveness, health and masculinity ratings. There was a significant inverse relationship between C and attractiveness ($\beta = -0.36$, $p = 0.027$; table 1).

The relationship between T and C was non-significant ($\beta = 0.09$, $p = 0.61$), so it was not possible to investigate mediation. Moderation was explored by centring T and C levels and creating an interaction term. Hierarchical

Table 1. The table shows β coefficients and multiple regression model adjusted r^2 values for relationships between T and C and attractiveness, masculinity and health ratings with and without inclusion of the $T \times C$ interaction term. (Asterisk indicates significance at 0.05 level.)

	model with T and C as predictors			model with interaction term included	
	adjusted r^2	T (ng ml ⁻¹)	C (nmol l ⁻¹)	adjusted r^2	T $\times$ C
attractiveness	0.08*	0.061	-0.36*	0.063	-0.08
masculinity	0.012	0.251	-0.052	0.017	-0.176
health	0.002	0.025	-0.234	0.002	-0.039

regression models were conducted with the centred T and C scores in the first level and the interaction term in the second. The addition of the interaction term did not explain significantly more of the variance in attractiveness, masculinity or health (all $p > 0.3$; table 1).

(e) Discussion

Relationships between T and C and ratings of attractiveness, masculinity and health of male faces were explored. There was no relationship between T and C, and ratings of faces, although the two may only relate at peak levels in humans [39]. T did not predict ratings of attractiveness, health or masculinity. C did not predict ratings of health or masculinity. There was a significant inverse relationship between C and attractiveness, such that faces of participants high in C were rated as less attractive than those low in C. This is consistent with the research which has shown female zebra finches to prefer males with low C [33]. We did not find evidence for mediation or moderation. Therefore, while results demonstrate a relationship between C and attractiveness of male faces, they do not demonstrate any effects of T and C in combination. The study, however, may have been limited by (i) the range of T and C in the sample and (ii) between-subjects variation in, for example, the cycle phase of female raters. The aim of Study 2 was to provide a stronger test of the ways in which T and C act together to influence attractiveness by isolating cues to high and low T and C in the face and measuring female preferences for stimuli that differ in combinations of these across the menstrual cycle.

3. STUDY 2

(a) Methods

(i) Facial stimuli

The 39 male faces described in study 1 were split into four groups based on T levels (using median and inter-quartile range), and four groups based on C levels. These groupings were then used to identify faces of males with high and low in C and T in order to construct the following four composite faces: high T and high C (HiTHiC), high T and low C (HiTLoC), low T and high C (LoTHiC) and low T and low C (LoTLoC). HiTHiC was constructed from eight faces (T: 0.41 (0.11); C: 16.51 (4.27)), HiTLoC from eight faces (T: 0.39 (0.07); C: 6.54 (1.32)), LoTHiC from six faces (T: 0.2 (0.06); C: 16.61 (4.97)) and LoTLoC from eight faces (T: 0.19 (0.06); C: 6.73 (1.9)). T and C levels differed significantly in desired directions between high and low composites (all $p < 0.01$). There were no significant differences in the ages of faces that comprised

Figure 1. Composite male faces constructed to differ in levels of T and C, with (from left to right) HiTHiC, HiTLoC, LoTHiC and LoTLoC.

composites (all $p > 0.3$). For details on the construction of composite faces, see [41]. For composites, see figure 1.

Four male base faces (images that were the average of four to five individual faces chosen at random from two image sets) were transformed 50 per cent towards each of the composites. This resulted in 16 facial stimuli (i.e. four faces that had been transformed towards each of the four composites).

(ii) Participants

Forty-three heterosexual female students from the University of Abertay Dundee (mean age: 26.28, s.d.: 7.55) took part during both fertile and non-fertile phases of their menstrual cycles. Participants did not use hormonal contraceptives, were not pregnant and had regular cycles of 25–36 days duration.

(iii) Materials and procedure

Participants reported number of days between onset of two consecutive periods of menstrual bleeding and number of days since onset of last menstruation. Cycle phase was calculated using the countback method in which ovulation is assumed to occur 14 days prior to the onset of the second period of bleeding. Zero to 7 days prior to ovulation were treated as 'late follicular' (fertile) and the days between ovulation and onset of next period of bleeding were treated as 'luteal' (non-fertile). Participants rated the facial stimuli (displayed in random order) for attractiveness on 1–7 scales during fertile and non-fertile phases.

(b) Results

Mean attractiveness ratings were calculated for HiTHiC, HiTLoC, LoTHiC and LoTLoC faces for each participant in each phase. ANOVA for repeated measures with T and C (high and low) and cycle phase (fertile and non-fertile) revealed a significant main effect of C on attractiveness ($F_{1,42} = 5.11$, $p = 0.029$) with faces with cues to low C receiving higher ratings ($M = 3.69$) than those with cues to high C ($M = 3.55$). There was a

Figure 2. Mean attractiveness ratings (± 1 s.e.) of facial composites constructed to differ in levels of T and C during non-fertile (white) and fertile (grey) phases of the menstrual cycle.

significant interaction between T and C ($F_{1,42} = 12.47$, $p = 0.001$) such that the faces with cues to high levels of both hormones and low levels of both hormones were rated as more attractive than those with cues to high levels of one and low levels of the other. Post hoc pairwise comparisons (with Bonferroni correction) demonstrated significant differences between the HiTHiC and LoTHiC faces and the LoTHiC and LoTLoC faces ($p < 0.001$). There was a significant interaction between T, C and cycle phase ($F_{1,42} = 4.45$, $p = 0.041$). Figure 2 shows that the pattern of interaction between the hormones described above held in the non-fertile, but not the fertile, phase. To further explore the interaction, the effects of T and C on attractiveness were analysed separately for each cycle phase. The interaction between the hormones was significant in the non-fertile phase ($F_{1,42} = 19.25$, $p < 0.001$) but not in the fertile phase ($p > 0.1$). There was a significant main effect of C in the fertile phase ($F_{1,42} = 6.44$, $p = 0.015$) but not in the non-fertile phase ($p > 0.1$).

4. GENERAL DISCUSSION

We investigated the effects of T and C on male facial attractiveness, testing predictions of the ICHH (females will prefer cues to T in male faces during the fertile phase of the menstrual cycle) and the SL-ICHH (C will influence the relationship between T and attractiveness). In Study 1, we investigated relationships between levels of T and C and ratings of attractiveness, masculinity and health in raw male faces. In Study 2, we created composite faces that were parametrically manipulated on cues to naturally co-occurring levels of T and C and compared preferences across the cycle. In both studies, females preferred faces with cues to low C but expressed no preference for cues to T alone. In Study 2, this effect remained during the fertile, but not the non-fertile, menstrual cycle phase. In the non-fertile cycle phase, preferences for cues to each hormone were contingent upon co-occurring levels of the other: cues to low levels of T and C were significantly more attractive when coupled with low levels of the other, and high levels of T and C were significantly more attractive when coupled with high levels of the other. All faces were rated as more attractive during the non-fertile phase, although the main effect of phase was not significant and could not account for differences in relative preferences. To summarize, preferences for cues to low C are stronger

in the fertile phase of the cycle, with a more complex interaction between the two hormones during the non-fertile phase.

Our results were more consistent with the SL-ICHH. We found no clear relationships between T and attractiveness, whereas cues to low C were rated as significantly more attractive than cues to high C in both studies. This is consistent with Roberts *et al.* [33] who found female zebra finches to prefer males with low C but to express no preference for T and suggested that low C males provide offspring with heritable benefits such as an optimum C response to support fight-or-flight while exerting minimum immunosuppression. Our results support this interpretation as, in humans, peak C is heritable (e.g. [42]) and suppresses the immune system (e.g. [38]). Furthermore, the preferences for cues to low C were only significant in the fertile cycle phase which, in the facial attractiveness literature, is treated as the context under which women judge faces on the basis of acquisition of heritable benefits for offspring (e.g. [13]). In order to test this 'good genes' interpretation, however, it would be necessary to assess relationships between markers of genetic quality (e.g. major histocompatibility complex heterozygosity, [9]) and hormonal profiles.

The SL-ICHH does not simply predict an effect of stress hormones on attractiveness, but that T and C will interact to predict immune response and trait expression. While we found no support for this in Study 1, the effects of T and C on attractiveness were contingent upon levels of the other in Study 2, at least during the non-fertile phase of the cycle. Faces with cues to low T were rated as more attractive when coupled with cues to low C than when coupled with cues to high C. Women also rated the faces of men with high C as more attractive when coupled with cues to high T than when coupled with cues to low T, which is consistent with Roberts *et al.* [31] who found the immune response of each hormone to be enhanced when co-occurring levels of the other were high. In our sample, this interaction existed only in the non-fertile cycle phase. In human research, this is treated as the context under which women judge faces on the basis of 'partnership' qualities such as current health or parenting qualities (e.g. [43]). That the stronger preferences for cues to high C with high T and cues to low C with low T were specific to the non-fertile phase, then, suggest that these combinations signal characteristics more heavily weighted in female mate-choice decisions when conception risk is low. Roberts *et al.* [31] suggested that males high in T and C are better able to compete for, and use, resources so can mount a stronger immune response. Perhaps, then, women in our sample prefer cues to resource acquisition during the non-fertile phase of the cycle, or to good current health. Women also preferred cues to low T significantly more when coupled with low C during the non-fertile phase, which may also be indicative of an individual with a good current health (e.g. with low immunosuppression and stress). Future research should investigate relationships between T and C and current health, immunocompetence and personality characteristics of males.

Our results inform the SL-ICHH by (i) demonstrating an interaction between T and C on attractiveness and (ii) indicating the traits that may be signalled by different combinations of the hormones. Our results were more

consistent with the interaction demonstrated by Roberts *et al.* [31], than with covariance of T and C [25]. We argue that the mechanisms by which the two hormones interact cannot simply be attributed to their covariance, and that an SL-ICHH must account for complexity in interactions between sex- and stress- hormones [25,31,32]. Evans [34] argues that the effects of T and C on behaviour will be species- and context-dependent. Our results have been interpreted in the context of a biparental mammalian species in which baseline T and C are not consistently related. As such, any interaction between the two on attractiveness is unlikely to be owing to their covariance and will reflect the mating strategies of human females. That is not to say that our results cannot inform application of the model to other species. On the contrary, that the interaction between the hormones occurred only in the non-fertile cycle phase informs as to the qualities signalled by combinations of the hormones, and we argue that cues to high C with high T and low C with low T may signal resource acquisition and/or current health. Furthermore, that preferences for cues to low C were strongest in the fertile phase lend support to a 'good genes' interpretation [33]. Results should be used to generate specific predictions regarding the value of different combinations of T and C in mate-choice decisions across species and contexts. Exploring preferences for these hormones across ecologies and endocrinological profiles will facilitate expansion of the model to better explain the role of stress in sexual selection.

While we found different patterns of preferences in the fertile and non-fertile phases, there were no interactions between cues to T or C alone and cycle phase. This is inconsistent with the results of previous studies which have found shifts in female preferences for cues to T across the menstrual cycle (e.g. [13–15]). Such studies, however, have typically shown a shift from preferences for slightly feminized faces in the non-fertile phase to preferences for less feminized or slightly masculinized faces in the non-fertile phase. It may be that our use of the faces of males with the highest T levels in our high T composites resulted in stimuli that were not considered attractive, even during the fertile phase of the cycle. Further tests using stimuli that have been exposed to a more subtle manipulation for cues to T would demonstrate whether there were any interactions between cues to T and C in, for example, the fertile phase which the current study failed to detect. Furthermore, we do not know which cues our raters attended to when judging faces. In the zebra finch, preferences for males with low C were based on leg, beak and cheek patch coloration and brightness [33]. T in humans is related to facial structure (e.g. [44]) and perceived dominance [45], and facial masculinity is related to perceived behavioural characteristics including honesty [46] and dominance (e.g. [47]). Facial skin coloration is related to perceived dominance [48,49]. It seems likely, then, that combinations of T and C cause variation in facial structure, skin colour/texture or cues to behaviour. Colour and skin patch analysis, as well as investigation of perceptions of personality traits of facial stimuli that differ in levels of T and C will further inform as to the traits that underlie women's preferences for cues to T and C.

In conclusion, our results do not support the original ICHH but are consistent with a stress-linked version of the model. The pattern of results suggests that the role of C in relationships between T and trait expression is not the result of covariance, supports a 'good genes' interpretation of female preferences for males with low C, and suggests that combinations of T and C signal underlying characteristics such as current health, immune response or resource acquisition. These results should inform the direction of future research into relationships between sex- and stress-hormones across species.

The research was fully approved by the ethics committee of the School of Psychology, University of St Andrews and the ethics committee of the School of Social and Health Sciences, University of Abertay, Dundee.

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REFERENCES

- 1 Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* **139**, 603–622. (doi:10.1086/285346)
- 2 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)
- 3 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)
- 4 Pound, N., Penton Voak, I. S. & Surridge, A. K. 2009 Testosterone responses to competition in men are related to facial masculinity. *Proc. R. Soc. B* **276**, 153–159. (doi:10.1098/rspb.2008.0990)
- 5 Fink, B. & Penton-Voak, I. S. 2002 Evolutionary psychology of facial attractiveness. *Curr. Dir. Psychol. Sci.* **11**, 154–158. (doi:10.1111/1467-8721.00190)
- 6 Gangestad, S. W., Thornhill, R. & Garver-Apgar, C. E. 2005 Adaptations to ovulation. *Curr. Dir. Psychol. Sci.* **14**, 312–316. (doi:10.1111/j.0963-7214.2005.00388.x)
- 7 Rhodes, G., Chan, J., Zebrowitz, L. A. & Simmons, L. W. 2003 Does sexual dimorphism in human faces signal health? *Proc. R. Soc. Lond. B* **270**, S93–S95. (doi:10.1098/rsbl.2003.0023)
- 8 Thornhill, R. & Gangestad, S. W. 2006 Facial sexual dimorphism, developmental stability and parasitic infections in men and women. *Evol. Hum. Behav.* **27**, 131–144. (doi:10.1016/j.evolhumbehav.2005.06.001)
- 9 Roberts, C., Little, A. C., Morris Gosling, L., Perrett, D. I., Carter, V., Jones, B. C., Penton Voak, I. & Petrie, M. 2005 MHC-heterozygosity and human facial attractiveness. *Evol. Hum. Behav.* **26**, 213–226. (doi:10.1016/j.evolhumbehav.2004.09.002)
- 10 Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCullough, J. K. & Franklin, M. 2003 Major histocompatibility genes, symmetry and body scent attractiveness in men and women. *Behav. Ecol.* **14**, 668–678. (doi:10.1093/beheco/arg043)
- 11 Rhodes, G. 2006 The evolutionary psychology of facial beauty. *Ann. Rev. Psychol.* **57**, 199–226. (doi:10.1146/annurev.psych.57.102904.190208)

- 12 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)
- 13 Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Female preference for male faces changes cyclically. *Nature* **399**, 741–742. (doi:10.1038/21557)
- 14 Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001 Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evol. Hum. Behav.* **22**, 251–267. (doi:10.1016/S1090-5138(01)00066-6)
- 15 Little, A. C., Jones, B. C. & DeBruine, L. M. 2008 Preferences for variation in masculinity in real male faces change across the menstrual cycle. *Pers. Individ. Differ.* **45**, 478–482. (doi:10.1016/j.paid.2008.05.024)
- 16 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)
- 17 DeBruine, L. M., Jones, B. C., Smith, F. G. & Little, A. C. 2010 Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *J. Exp. Psych. Hum. Percept. Perform.* **36**, 751–758. (doi:10.1037/a0016457)
- 18 Buchanan, K. L., Evans, M. R. & Goldsmith, A. R. 2003 Testosterone, dominance signalling and immunosuppression in the house sparrow, *Passer domesticus*. *Behav. Ecol. Sociobiol.* **55**, 50–59. (doi:10.1007/s00265-003-0682-4)
- 19 Deviche, P. & Cez, L. 2005 Androgen control of immunocompetence in the male house finch, *Carpodacus mexicanus*. *J. Exp. Biol.* **208**, 1287–1295. (doi:10.1242/jeb.01531)
- 20 Chen, K. L., Tsay, S. M., Chiou, P. W. S., Chen, T. W. & Weng, B. C. 2009 Effects of castration and testosterone implantation on immunity in male chickens. *Poult. Sci.* **88**, 1832–1837. (doi:10.3382/ps.2009-00104)
- 21 Hasselquist, D., Marsh, J. A., Sherman, P. W. & Wingfield, J. C. 1999 Is avian humoral immunocompetence suppressed by testosterone? *Behav. Ecol. Sociobiol.* **45**, 167–175. (doi:10.1007/s002650050550)
- 22 Greenman, C. G., Martin, L. B. & Hau, M. 2005 Reproductive state, but not testosterone, reduces immune function in male house sparrow (*Passer domesticus*). *Physiol. Biochem. Zool.* **78**, 60–68. (doi:10.1086/425194)
- 23 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)
- 24 Møller, A. P. 1995 Hormones, handicaps and bright birds. *Trends Ecol. Evol.* **10**, 121. (doi:10.1016/S0169-5347(00)89008-4)
- 25 Evans, M. R., Goldsmith, A. R. & Norris, S. R. A. 2000 The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav. Ecol. Sociobiol.* **47**, 156–163. (doi:10.1007/s002650050006)
- 26 Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S. E., Ramenofsky, M. & Richardson, R. D. 1998 Ecological bases of hormone-behavior interactions: the emergency life history stage. *Am. Zool.* **38**, 191–206.
- 27 Buchanan, K. L. 2000 Stress and the evolution of condition dependent signals. *Trends Ecol. Evol.* **15**, 157–160. (doi:10.1016/S0169-5347(99)01812-1)
- 28 Sapolsky, R. M., Romero, M. & Munck, A. U. 2000 How do glucocorticoids influence stress response? Integrating permissive, suppressive, stimulatory, and preparative actions. *End. Rev.* **21**, 55–89. (doi:10.1210/er.21.1.55)
- 29 Breuner, C. W., Greenberg, A. L. & Wingfield, J. C. 1998 Noninvasive Ciccosterone treatment rapidly increases activity in Gambel's white-crowned sparrows. *Gen. Comp. Endocrinol.* **111**, 386–395. (doi:10.1006/gcen.1998.7128)
- 30 Nepomnaschy, P. A., Welch, K., McConnell, D., Strassman, B. I. & England, B. G. 2004 Stress and female reproductive function: a study of daily variations in Cortisol, gonadotropins, and gonadal steroids in a rural Mayan population. *Am. J. Hum. Biol.* **16**, 523–532. (doi:10.1002/ajhb.20057)
- 31 Roberts, M. L., Buchanan, K. L., Hasselquist, D. & Evans, M. R. 2007 Effects of testosterone and corticosterone on immunocompetence in the zebra finch. *Horm. Behav.* **51**, 126–134. (doi:10.1016/j.yhbeh.2006.09.004)
- 32 Roberts, M. L., Buchanan, K. L., Evans, M. R., Marin, R. H. & Satterlee, D. G. 2009 The effects of testosterone on immune function in quail selected for divergent plasma Ciccosterone response. *J. Exp. Biol.* **212**, 3125–3131. (doi:10.1242/jeb.030726)
- 33 Roberts, M. L., Buchanan, K. L., Bennett, A. T. D. & Evans, M. R. 2007 Mate choice in zebra finches: does corticosterone play a role? *Anim. Behav.* **74**, 921–929. (doi:10.1016/j.anbehav.2006.12.021)
- 34 Evans, M. R. 2010 Why does testosterone influence morphology, behaviour and physiology? *Open Ornithol. J.* **6**, 21–26.
- 35 Grossman, C. J. 1995 The role of sex steroids in immune system regulation. In *Bilateral communication between the endocrine and immune systems* (ed. C. J. Grossman), pp. 1–11. New York, NY: Springer.
- 36 Kanda, N., Tsuchida, T. & Tamaki, K. 1996 Testosterone inhibits immunoglobulin production by human peripheral blood mononuclear cells. *Clin. Exp. Immunol.* **106**, 410–415. (doi:10.1046/j.1365-2249.1996.d01-842.x)
- 37 Muehlenbein, M. P. & Bribiescas, R. G. 2005 Testosterone mediated immune functions and male life history traits. *Am. J. Hum. Biol.* **17**, 527–558. (doi:10.1002/ajhb.20419)
- 38 Bauer, M. E., Moriguchi Jeckel, C. M. & Luz, C. 2009 The role of stress factors during aging of the immune system. *Ann. NY Acad. Sci.* **1153**, 139–152. (doi:10.1111/j.1749-6632.2008.03966.x)
- 39 Brownlee, K. Y., Moore, A. W. & Hackney, A. C. 2005 Relationship between circulating cortisol and testosterone: influence of physical exercise. *J. Sports Sci. Med.* **1**, 76–83.
- 40 Al-Dujaili, E. A. S. 2006 Development and validation of a simple and direct ELISA method for the determination of conjugated (glucuronide) and non-conjugated testosterone excretion in urine. *Clin. Chim. Acta* **364**, 172–179.
- 41 Tiddeman, B. T., Burt, D. M. & Perrett, D. I. 2001 Prototyping and transforming facial textures for perception research. *Comput. Graph. Appl.* **21**, 42–50. (doi:10.1109/38.946630)
- 42 Steptoe, A., Van Jaarsveld, C. H. M. & Semmler, C. 2009 Heritability of daytime cortisol levels and cortisol reactivity in children. *Psychoneuroendocrinology* **34**, 273–280. (doi:10.1016/j.psyneuen.2008.09.006)
- 43 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)

- 44 Enlow, A. H. 1990 *Facial growth*. Philadelphia, PA: WB Saunders Company.
- 45 Swaddle, J. P. & Reiersen, 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)
- 46 Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* **394**, 884–887. (doi:10.1038/29772)
- 47 Mazur, A. & Booth, A. 1998 Testosterone and dominance in men. *Behav. Brain Sci.* **21**, 353–397.
- 48 Stephen, I. D., Coatzee, V., Law Smith, M. J. & Perrett, D. I. 2009 Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE* **4**, e5083. (doi:10.1371/journal.pone.0005083)
- 49 Stephen, I. D., Law Smith, M. J., Stirrat, M. & Perrett, D. I. 2009 Facial skin coloration affects perceived health of human faces. *Int. J. Primatol.* **30**, 845–857. (doi:10.1007/s10764-009-9380-z)