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Men report stronger attraction to femininity in women's faces when their testosterone levels are high

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ABSTRACT

Many studies have shown that women's judgments of men's attractiveness are affected by changes in levels of sex hormones. However, no studies have tested for associations between changes in levels of sex hormones and men's judgments of women's attractiveness. To investigate this issue, we compared men's attractiveness judgments of feminized and masculinized women's and men's faces in test sessions where salivary testosterone was high and test sessions where salivary testosterone was relatively low. Men reported stronger attraction to femininity in women's faces in test sessions where salivary testosterone was high than in test sessions where salivary testosterone was high than in test sessions where salivary testosterone was low. This effect was found to be specific to judgments of opposite-sex faces. The strength of men's reported attraction to femininity in men's faces did not differ between high and low testosterone test sessions, suggesting that the effect of testosterone that we observed for judgments of women's faces was not due to a general response bias. Collectively, these findings suggest that changes in testosterone levels contribute to the strength of men's reported attraction to femininity in women's faces and complement previous findings showing that testosterone modulates men's interest in sexual stimuli.

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Introduction

Many studies have demonstrated cyclic variation in the strength of women's reported attraction to putative cues of men's underlying health (see Gangestad and Thornhill (2008) and Jones et al. (2008) for recent reviews). For example, women report stronger attraction to masculine characteristics in men's faces (Frost, 1994; Johnston et al., 2001; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Welling et al., 2007), voices (Feinberg et al., 2006; Puts, 2006), and bodies (Little et al., 2007) during the late follicular phase of the menstrual cycle than at other times. Women also rate the attractiveness of androstenone (a male pheromone, Grammer, 1993), videoclips of male behavioral displays of dominance (Gangestad et al., 2004), and the scent of symmetric men (Garver-Apgar et al., 2008; Thornhill and Gangestad, 1999; Thornhill et al., 2003) higher during the late follicular phase of the menstrual cycle than during other phases. Stronger attraction to these putative cues of men's underlying health during the late follicular (i.e., fertile) phase of the menstrual cycle may be adaptive because it is likely to increase offspring health (see Gangestad and Thornhill (2008) and Jones et al. (2008) for reviews).

Recent research has focused on investigating the hormonal changes that are associated with cyclic shifts in women's judgments of men's attractiveness (see, e.g., Garver-Apgar et al., 2008; Jones et al., 2005; Puts, 2006; Welling et al., 2007). Several studies have found negative relationships between progesterone level during the menstrual cycle and the strength of women's reported attraction to masculine or symmetric men (Garver-Apgar et al., 2008; Jones et al., 2005; Puts, 2006; Welling et al., 2007). Other studies have reported positive relationships between estrogen (Garver-Apgar et al., 2008; Roney and Simmons, 2008) and testosterone (Welling et al., 2007) levels during the menstrual cycle and women's ratings of the attractiveness of masculine or symmetric men. While these findings have provided important insights into the hormonal mechanisms that may underpin variation in women's judgments of men's attractiveness (Gangestad and Thornhill, 2008; Jones et al., 2008), we know of no studies that have tested for associations between changes in hormone levels and changes in men's judgments of women's facial attractiveness.

Van Honk et al. (1999) found that testosterone level is positively associated with men's attention to socially relevant stimuli. More recently, Rupp and Wallen (2007) reported a positive relationship

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Fig. 1. Examples of masculinized (left) and feminized (right) face images and the interface used in our study to assess the strength of men's attraction to feminine faces.

between testosterone level and men's interest in sexual stimuli (as measured by self-regulated viewing times for pornographic images). These findings raise the possibility that men may report stronger attraction to femininity in women's faces, a characteristic that is sexually attractive to men (Jones et al., 2007; Perrett et al., 1998; Rhodes, 2006), when testosterone level is high than when testosterone level is relatively low. Indeed, findings from studies reporting positive associations between men's interest in high sensation activities and both their testosterone levels (Aluja and Torrubia, 2004) and the strength of their reported attraction to femininity in women's faces (Jones et al., 2007) also suggest that there may be an association between testosterone and the strength of men's reported attraction to femininity in women's faces.

In light of the above, we investigated the relationship between changes in endogenous testosterone levels and the strength of men's reported attraction to femininity in women's faces. Using a within-subjects design and natural fluctuations in testosterone, we compared the strength of men's reported attraction to femininity (vs. masculinity) in test sessions where testosterone levels were high ('high testosterone test sessions') and test sessions where testosterone levels were relatively low ('low testosterone test sessions'). We predicted that men's reported attraction to femininity in women's faces would be stronger in high testosterone test sessions than in low testosterone test sessions. However, since systematic variation in the strength of men's reported attraction to femininity in women's faces has previously been found to occur for judgments of women's, but not men's, faces (Jones et al., 2007), we did not necessarily anticipate an effect of testosterone level on attractiveness judgments of men's faces. The methods that we used to assess the strength of men's attraction to femininity in women's faces are identical to those that have previously been used to demonstrate hormonal effects on women's judgments of the attractiveness of masculinized vs. feminized men's faces (e.g., Jones et al., 2005; Welling et al., 2007).

Methods

Stimuli

Following previous studies of systematic variation in men's and women's judgments of the attractiveness of feminine and masculine faces (Buckingham et al., 2006; DeBruine et al., 2006; Jones et al., 2005, 2007; Penton-Voak et al., 1999; Little et al., 2005; Welling et al., 2007, 2008), we used prototype-based image transformations to

objectively manipulate sexual dimorphism of 2D shape in digital face images. Although different methods for manipulating masculinity of face images have been used in some other studies (e.g., Johnston et al., 2001), these methods have been shown to produce effects on attractiveness judgments that are equivalent to those produced using the methods in our current study (DeBruine et al., 2006).

First, male and female prototype (i.e., average) faces were manufactured using established computer graphic methods that have been widely used in studies of face perception (e.g., DeBruine et al., 2006; Jones et al., 2005, 2007; Penton-Voak et al., 1999; Welling et al., 2007, 2008). Prototypes are composite images that are constructed by averaging the shape, color and texture of a group of faces, such as male or female faces. These prototypes can then be used to transform images by calculating the vector differences in position between corresponding points on two prototype images and changing the position of the corresponding points on a third image by a given percentage of these vectors (see Rowland and Perrett (1995), Tiddeman et al. (2001) for technical details).

Here, 50% of the linear differences in 2D shape between symmetrized versions of the male and female prototypes were added to or subtracted from face images of 20 young White male adults (age: M=19.5 years, SD=2.3 years) and 20 young White female adults (age: M=18.4 years, SD=0.7 years). This process creates masculinized and feminized versions of the individual face images that differ in sexual dimorphism of 2D shape and that are matched in other regards (e.g., identity, skin color and texture, Rowland and Perrett, 1995). Examples of masculinized and feminized face images are shown in Fig. 1. Thus, 40 pairs of images were produced in total (each pair consisting of a masculinized and a feminized version of the same individual): 20 pairs of female face images and 20 pairs of male face images.

Manipulation check

We carried out a pilot study to establish whether or not manipulating sexual dimorphism of 2D shape in our stimuli influenced perceptions of their femininity in the predicted way. Participants (*N*=29, all male, age: M=23.07 years, SD=4.98 years) viewed the 40 pairs of face images (each pair consisting of the masculinized and feminized versions of the same individual) and were asked to choose the face in each pair that looked more feminine. The order of face pairs was fully randomized, as was the side of the screen on which any given image was shown. This two-

alternative forced choice method produces a single score for each participant (the number of trials on which the more feminine face in each pair was chosen). One-sample t-tests confirmed that the feminized versions were chosen as the more feminine face more often than the chance value of 10 for both female (t(28)=22.37, p<.001; M=17.97, SE=0.36) and male faces (t(28)=21.10, p<.001; M=18.83, SE=0.42), confirming that our image manipulation influenced perceptions of facial femininity in the predicted way (see also DeBruine et al., 2006; Perrett et al., 1998; Welling et al., 2007).

Procedure

Male participants (*N*=29; age: M=20.48 years, SDM=3.56 years) were tested on two occasions. None of the men who participated in the main experiment had participated in the manipulation check. The second test session took place two weeks after the first test session. Although the time of day in which test sessions took place differed across men, the time of day of test sessions remained constant within each participant. Test sessions took place between 10 am and 4 pm. All participants were undergraduate students at the University of Aberdeen who were participating in the study in return for course credit. All participants described their sexual orientation as exclusively heterosexual.

In each test session, participants were shown the 40 pairs of face images (20 male and 20 female) and were asked to choose the face in each pair that was more attractive. Each pair of images consisted of masculinized and feminized versions of the same individual. Participants were also instructed to indicate the extent to which the chosen face was more attractive by choosing from the options 'slightly more attractive', 'somewhat more attractive', 'more attractive', and 'much more attractive' (see Fig. 1). The specific instructions given at the start of the test were: "In this experiment you will be asked to choose which face in a pair looks more attractive. The faces will all look very similar, but they are each subtly different. Indicate how much more attractive you think it looks by clicking on one of the buttons above the face. If you have any questions, please ask the experimenter now." On each trial, additional instructions given were: "Please indicate which face you think is more attractive (and how much you prefer it) by clicking on one of the phrases above the face you prefer." These instructions were presented on the computer monitor. No participants asked for clarification of the

The order in which pairs of faces were shown was fully randomized for each participant and the side of the screen on which any particular image was shown was also randomized. This method for assessing judgments of facial attractiveness has been used in many previous studies of variation in judgments of the attractiveness of masculinized and feminized faces (e.g., Buckingham et al., 2006; Jones et al., 2005, 2007).

Participants deposited between 3 and 5 mL of saliva by spitting directly into plastic pharmaceutical vials at the beginning of each testing session. The vials were then sealed and frozen at -20° C until analysis.

Testosterone assay data

Hormonal assays were performed by the biological sciences lab at Queen Margaret University (Edinburgh, UK). Salivary testosterone levels were determined by a highly sensitive and specific in-house ELISA method (Al-Dujaili, 2006). Briefly, saliva samples were first extracted with diethylether and 100 µL aliquots of the re-constituted samples. Standards and controls were then pipetted into the 96-well pre-coated ELISA plate. The procedure was then completed as previously described (Al-Dujaili, 2006). Previous studies have confirmed the validity of the assay by the extremely high correlation

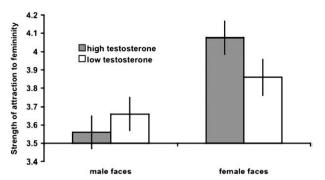


Fig. 2. The significant interaction between *test session* and *sex of face judged* in our main analysis (rating scale data). Men's reported attraction to femininity in women's faces was stronger in the high testosterone test session than in the low testosterone test session. By contrast, there was no corresponding difference for judgments of men's faces. On the *y*-axis, 3.5 equals chance. Bars show means and SEMs. Analyses of forced choice responses showed a similar pattern of results.

(R^2 =0.95) between the results obtained by the in-house ELISA and those assayed by the Salimetrics (USA) ELISA kit (Welling et al., 2007). In our sample of men, there was also an extremely high correlation between the testosterone ELISA values and those obtained after HPLC separation and ELISA (R^2 =0.96).

Initial processing of data

Salivary testosterone data were used to identify the test sessions with the highest and lowest salivary testosterone for each participant. Testosterone levels were significantly higher in the high testosterone session (M=1.09 nmol/L, SEM=0.04) than in the low testosterone session (M=0.89 nmol/L, SEM=0.04; t(28)=7.64, p<.001; mean difference=0.20 nmol/L, SEM=0.26). These testosterone levels are within population norms for young adult males assessed by this laboratory (Al-Dujaili, 2006). Allocating test sessions to high and low testosterone test sessions did not confound testosterone level and order of testing; the first test session was the high testosterone test session for 14 of the 29 participants, which is not significantly different to what would be expected by chance alone (Binomial test: p=.98).

Following Buckingham et al. (2006) and Jones et al. (2005, 2007), responses on the facial attractiveness test were coded using the following 0 to 7 scale:

- 0=masculine face rated 'much more attractive'
- 1 = masculine face rated 'more attractive'
- 2=masculine face rated 'somewhat more attractive'
- 3=masculine face rated 'slightly more attractive'
- 4=feminine face rated 'slightly more attractive'
- 5 = feminine face rated 'somewhat more attractive'
- 6=feminine face rated 'more attractive'
- 7 = feminine face rated 'much more attractive'

We then calculated the average score for judgments of women's faces for the high testosterone test session and the average score for judgments of men's faces for the high testosterone test session separately for each participant. Corresponding values for each participant were also calculated for the low testosterone test session. These four values were used in our main analyses (rating scale data).

In addition to the rating scale data described above, we also calculated the number of trials (out of 20 possible) on which each participant chose the feminized version when judging male faces in the high testosterone test session, male faces in the low testosterone test session, female faces in the high testosterone

Table 1Pairwise comparisons for forced choice data (number of times feminine faces were chosen as more attractive out of 20 maximum)

Comparison		Comparison means (SEMs)		t(28)	р
Women's faces (high testosterone session)	Women's faces (low testosterone session)	14.28 (0.61)	13.10 (0.63)	1.75	.091
Men's faces (high testosterone session)	Men's faces (low testosterone session)	10.72 (0.76)	11.69 (0.70)	-1.38	.177
Women's faces (high testosterone session)	Men's faces (high testosterone session)	14.28 (0.61)	10.72 (0.76)	4.49	<.001
Women's faces (low testosterone session)	Men's faces (low testosterone session)	13.10 (0.63)	11.69 (0.70)	2.24	.033

The Bonferroni critical p-value for these comparisons is .0125.

test session, and female faces in the low testosterone test session. This forced choice data was used in our supplementary analyses (forced choice data).

Results

Main analyses (rating scale data)

Repeated measures ANOVA [dependent variable: rated strength of attraction to femininity; within-subjects factors: *test session* (high testosterone, low testosterone); *sex of face judged* (male, female)] revealed a significant interaction between *test session* and *sex of face judged* (F(1,28)=9.20, p=.005, see Fig. 2). Planned comparisons using paired-samples t-tests were then carried out to test whether this interaction reflected stronger reported attraction to femininity in the high testosterone test session than in the low testosterone test session when judging women's faces, but not when judging men's faces. These analyses showed that men reported stronger attraction to feminized faces in the high testosterone test session than in the low testosterone test session when judging women's faces (t(28)=2.14, t=0.041), but not when judging men's faces (t(28)=-1.25, t=0.041), but not when judging men's faces (t(28)=-1.25, t=0.041), but not when judging men's faces (t(28)=-1.25, t=0.041), but not when

In addition to the significant interaction between *test session* and *sex of face judged*, the repeated measures ANOVA also showed a significant main effect of *sex of face judged* (F(1,28)=18.12, p<.001). This significant main effect of *sex of face judged* reflected stronger attraction to femininity in female faces (M=3.97, SEM=0.08) than in male faces (M=3.61, SEM=0.08). The main effect of *test session* was not significant (F(1,28)=0.53, p=.48).

We then used one-sample *t*-tests to compare the reported strength of attraction to feminized (vs. masculinized) faces with what would be expected by chance alone (i.e., what would be expected if there was no significant bias in attraction to feminized vs. masculinized faces) separately for each of the four conditions: male faces judged in the high testosterone test session, male faces judged in the low testosterone test session, female faces judged in the high testosterone test session, and female faces judged in the low testosterone test session. These one-sample t-tests comparing the strength of attraction to feminine (vs. masculine) faces with what would be expected by chance alone (i.e., 3.5) showed that participants reported stronger attraction to feminine female faces than to masculine female faces in both the high (t(28)=6.27,p<.001) and low (t(28)=3.64, p=.001) testosterone test sessions. Corresponding analyses for judgments of male faces showed that participants tended to report stronger attraction to feminine male faces than to masculine male faces in the low testosterone test sessions (t(28)=1.94, p=.063), but not in the high testosterone test sessions (t(28)=0.64, p=.53). Note, however, that the pairedsamples t-test reported above shows that this difference is not significant.

Supplementary analyses (forced choice data)

Next, we repeated these analyses for the number of trials on which the feminine versions of the faces were chosen as the more attractive (i.e., the forced choice data). Repeated measures ANOVA [dependent variable: number of trials on which feminine version was chosen; within-subjects factors: test session (high testosterone, low testosterone); sex of face judged (male, female)] revealed a significant interaction between test session and sex of face judged (F(1,28)=7.43,p=.011). Results of pairwise comparisons using paired-samples ttests were carried out to interpret this interaction and are shown in Table 1. The Bonferroni critical *p*-value for these comparisons is .0125. These pairwise comparisons suggest that the interaction between test session and sex of face judged reflected feminine women's faces being chosen more often than feminine men's faces in the high testosterone test session, but not in the low testosterone test session. The maximum number of times feminine faces could be chosen for judgments of men's or women's faces was 20.

The repeated measures ANOVA also showed a significant main effect of *sex of face judged* (F(1,28)=17.20, p<.001). This significant main effect of *sex of face judged* reflected feminine faces being chosen as the more attractive more often when judging women's faces (M=13.69, SEM=0.52) than when judging men's faces (M=11.21, SEM=0.65). The main effect of *test session* was not significant (F(1,28)=0.34, P=.86).

One-sample t-tests comparing the number of times the feminine versions of women's faces were chosen with the chance value of 10 showed that participants chose the feminine versions of women's faces as the more attractive significantly more often than the masculine versions in both the high (t(28)=6.99, p<.001) and low (t(28)=4.97, p<.001) testosterone test sessions. One-sample t-tests comparing the number of times the feminine versions of men's faces were chosen with the chance value of 10 also showed that participants chose the feminine versions of men's faces as the more attractive significantly more often than the masculine versions in the low testosterone test session (t(28)=2.41, p=.023), but not in the high testosterone test session (t(28)=0.95, p=.35).

 $Between-subjects\ variation\ in\ testosterone\ and\ attractiveness\ judgments$

Finally, we averaged scores across high and low testosterone sessions to test whether between-subjects variation in men's average testosterone levels predicted their judgments of men's and women's facial attractiveness. There were no significant correlations between men's average testosterone levels and the average scores for any of the attractiveness measures (see Table 2).

Discussion

Analyses of both the rating scale data and forced choice data showed that the men in our study generally demonstrated stronger attraction to femininity than masculinity in women's faces in both the high and low testosterone test sessions. This finding confirms that the men in our study considered femininity in women's faces attractive, replicating the findings of previous studies (e.g., Jones et al., 2007; Perrett et al., 1998; Rhodes, 2006).

 Table 2

 Results for correlations (Pearson) between average testosterone level and attractiveness measures

Attractiveness measure	Sex of face	r	p
Strength of reported attraction to femininity (0 to 7 scale data)	Male	-0.23	.24
Strength of reported attraction to femininity (0 to 7 scale data)	Female	-0.07	.71
Number of feminine faces chosen (forced choice data)	Male	-0.18	.36
Number of feminine faces chosen (forced choice data)	Female	0.13	.51

N=29 for each test.

Consistent with our prediction, analyses of the rating scale data also showed that men's reported attraction to femininity in women's faces was stronger in the high testosterone test sessions than in the low testosterone test sessions. By contrast with this finding for judgments of women's faces, analyses of the rating scale data revealed no significant difference in the strength of men's reported attraction to femininity in men's faces between the high and low testosterone test sessions. The absence of an effect of testosterone level on ratings of the attractiveness of men's faces suggests that our findings for reported strength of attraction to femininity in women's faces cannot be explained by a possible general response bias, whereby participants may have simply been more willing to use extreme points on the response scale when their testosterone levels were relatively high.

By contrast with the analyses of rating scale data described above, analyses of men's forced choice data revealed no significant effect of testosterone level on the number of times men chose the feminine faces as the more attractive for judgments of either men's or women's faces. However, the number of times the feminine face was chosen as more attractive was significantly greater for women's faces than for men's faces in the high testosterone test session, but not in the low testosterone test session. Together with our finding that men chose the feminine versions of women's faces as the more attractive significantly more often than the masculine versions in both the high and low testosterone test sessions, these findings suggest that men were not more likely to choose masculine women over feminine women when testosterone was low than when testosterone was high. That we found that men reported stronger attraction to femininity in women's faces when testosterone was high than when testosterone was low when we analyzed rating scale data, but were not more likely to choose feminine women as more attractive in the high testosterone test session, is unsurprising given the strong general attraction to femininity in women's faces that was observed in the current study, as well as in many previous studies (e.g., Jones et al., 2007; Perrett et al., 1998; Rhodes, 2006). This pattern of results is consistent with previous work on individual differences in men's attraction to femininity in women's faces, which has shown that men generally demonstrate strong attraction to femininity over masculinity in women's faces, but vary in the strength of attraction to femininity that they report (Jones et al., 2007).

We found no evidence that between-subjects variation in men's testosterone levels was associated with attractiveness judgments; there were no significant associations between average testosterone levels (calculated by averaging testosterone levels across the high and low testosterone test sessions) and the average scores for any of our attractiveness measures. We note, however, that 29 men is a relatively small sample for investigating between-subjects variation in men's attractiveness judgments of women's faces, so suggest that these null findings for between-subjects variation in testosterone should be treated with caution.

Stronger reported attraction to femininity in women's faces when testosterone levels are relatively high, as revealed by our analyses of men's rating scale data, complements previous studies reporting positive associations between testosterone and men's interest in sexual stimuli (e.g., Rupp and Wallen, 2007). Moreover, our findings also complement previous research implicating testosterone in men's attention to socially relevant stimuli (Van Honk et al., 1999) and in women's attractiveness judgments of faces in which sexual dimorphism had been manipulated (Welling et al., 2007). While many previous studies have reported associations between levels of sex hormones during the menstrual cycle and women's judgments of men's attractiveness (see Gangestad and Thornhill (2008) and Jones et al. (2008) for recent reviews), this is the first study that we know of to show an association between hormone levels and men's ratings of women's facial attractiveness.

Previous studies of cyclic shifts in women's attractiveness judgments of men's faces (e.g., Penton-Voak et al., 1999; Penton-Voak and

Perrett, 2000; Welling et al., 2007), voices (Feinberg et al., 2006; Puts, 2006), bodies (Little et al., 2007), and behavioral displays (Gangestad et al., 2004) have emphasized the possible benefits of increased attraction to male cues of underlying health during the fertile phase of the menstrual cycle (i.e., increased offspring health). Thus, it is interesting to consider the possible function of stronger reported attraction to femininity in women's faces when men's testosterone levels are relatively high. Attractive, feminine facial characteristics are associated with various indices of women's health and fertility (Henderson and Anglin, 2003; Hume and Montgomerie, 2001; Law Smith et al., 2006; Penton-Voak et al., 2003; Roberts et al., 2004; Thornhill and Gangestad, 2006). Positive associations between men's testosterone level and both their sexual interest (Rupp and Wallen, 2007) and the perceived strength of their attraction to femininity in women's faces may, therefore, function to promote mating with healthy, fertile women and, by extension, function to increase men's reproductive success. The possible function of the association between within-subjects variation in testosterone and the strength of men's reported attraction to femininity in women's faces is an interesting issue for future research. Additionally, while our study shows an association between within-subjects variation in testosterone and the reported strength of men's attraction to femininity in women's faces, further research is needed to clarify whether testosterone has a direct causal effect on men's attractiveness judgments or whether testosterone is associated with other factors that directly modulate attractiveness judgments of the opposite-sex.

Hormonal effects on women's judgments of men's attractiveness have proven to be an extremely fruitful line of research (Gangestad and Thornhill, 2008; Jones et al., 2008). Our findings for stronger reported attraction to femininity in women's faces when men's testosterone levels are relatively high suggest that the effects of changes in levels of sex hormones are not restricted to women's attractiveness judgments, however, but also modulate men's ratings of the attractiveness of feminine female faces. Indeed, our findings present novel evidence for the importance of hormone levels for social perception and suggest that endogenous testosterone level may be an important source of variation in men's perceptions of women's attractiveness.

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References

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.

Aluja, A., Torrubia, R., 2004. Hostility-aggressiveness, sensation seeking, and sex hormones in men: re-exploring their relationship. Neuropsychobiology 50, 102–107.

Buckingham, G., DeBruine, L.M., Little, A.C., Welling, L.L.M., Conway, C.A., Tiddeman, B.P., Jones, B.C., 2006. Visual adaptation to masculine and feminine faces influences generalized preferences and perceptions of trustworthiness. Evol. Hum. Behav. 27, 381–389.

DeBruine, L.M., Jones, B.C., Little, A.C., Boothroyd, L.G., Perrett, D.I., Penton-Voak, I.S., Cooper, P.A., Penke, L., Feinberg, D.R., Tiddeman, B.P., 2006. Correlated preferences for facial masculinity and ideal or actual partner's masculinity. Proc. R. Soc. Lond. B 273, 1355–1360.

Feinberg, D.R., Jones, B.C., Law Smith, M.J., Moore, F.R., DeBruine, L.M., Cornwell, R.E., Hillier, S.G., Perrett, D.I., 2006. Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. Horm. Behav. 49, 215–222.

Frost, P., 1994. Preference for darker faces in photographs at different phases in the menstrual cycle. Percept. Mot. Skills 79, 507–514.

Gangestad, S.W., Thornhill, R., 2008. Human oestrus. Proc. R. Soc. Lond. B 275, 991–1000.
Gangestad, S.W., Simpson, J.A., Cousins, A.J., Garver-Apgar, C.E., Christensen, P.N., 2004.
Women's preferences for male behavioral displays change across the menstrual cycle. Psychol. Sci. 15, 203–207.

Garver-Apgar, C.E., Gangestad, S.W., Thornhill, R., 2008. Hormonal correlates of women's mid-cycle preference for the scent of symmetry. Evol. Hum. Behav. 29, 223–232.

- Grammer, K., 1993. 5-alpha-androst-16en-3-alpha-on a male pheromone a brief report. Ethol. Sociobiol. 14, 201–207.
- Henderson, J.J.A., Anglin, J.M., 2003. Facial attractiveness predicts longevity. Evol. Hum. Behav. 24, 351–356.
- Hume, D.K., Montgomerie, R., 2001. Facial attractiveness signals different aspects of quality in men and women. Evol. Hum. Behav. 22, 93–112.
- 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.
- Jones, B.C., Little, A.C., Boothroyd, L., 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.
- Jones, B.C., DeBruine, L.M., Little, A.C., Conway, C.A., Welling, L.L.M., Smith, F.G., 2007. Sensation seeking and men's face preferences. Evol. Hum. Behav. 28, 439–446.
- Jones, B.C., DeBruine, L.M., Perrett, D.I., Little, A.C., Feinberg, D.R., Law Smith, M.J., 2008. Effects of menstrual cycle phase on face preferences. Arch. Sex. Behav. 37, 78–84.
- Law Smith, M.J., Perrett, D.I., Jones, B.C., Cornwell, R.E., Moore, F.R., Feinberg, D.R., Boothroyd, L.G., Durrani, S.J., Stirrat, M.R., White, S.R., Pitman, R.M., Hillier, S.G., 2006. Facial appearance is a cue to oestrogen levels in women. Proc. R. Soc. Lond. B 273, 135–140.
- Little, A.C., DeBruine, L.M., Jones, B.C., 2005. Sex-contingent face aftereffects suggest distinct neural populations code male and female faces. Proc. R. Soc. Lond. B 272, 1–5.
- Little, A.C., Jones, B.C., Burriss, R.P., 2007. Preferences for masculinity in male bodies change across the menstrual cycle. Horm. Behav. 52, 633–639.
- Penton-Voak, I.S., Perrett, D.I., 2000. Female preference for male faces changes cyclically further evidence. Evol. Hum. Behav. 21, 39–48.
- 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.
- 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*). J. Comp. Psychol. 117, 264–271.

- 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.
- Puts, D.A., 2006. Cyclic variation in women's preferences for masculine traits potential hormonal causes. Human Nat, 17, 114–127.
- Rhodes, G., 2006. The evolutionary psychology of facial beauty. Annu. Rev. Psychol. 57, 199–226
- Roberts, S.C., Havlicek, J., Flegr, J., Hruskova, M., Little, A.C., Jones, B.C., Perrett, D.I., Petrie, M., 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. Proc. R. Soc. Lond. B 271, 270–272.
- Roney, J.R., Simmons, Z.L., 2008. Women's estradiol predicts preference for facial cues of men's testosterone. Horm. Behav. 53, 14–19.
- Rowland, D.A., Perrett, D.I., 1995. Manipulating facial appearance through shape and color, IEEE Comput. Graph. Appl. 15, 70–76.
- Rupp, H.A., Wallen, K., 2007. Relationship between testosterone and interest in sexual stimuli: the effect of experience. Horm. Behav. 52, 581–589.
- Thornhill, R., Gangestad, S.W., 1999. Facial attractiveness. Trends Cogn. Sci. 3, 452–460. Thornhill, R., Gangestad, S.W., 2006. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. Evol. Hum. Behav. 27, 131–144.
- Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K., Franklin, M., 2003.
 Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behav. Ecol. 14. 668–678.
- Tiddeman, B., Burt, M., Perrett, D., 2001. Prototyping and transforming facial textures for perception research. IEEE Comput. Graph. Appl. 1, 42–50.
- Van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., 1999. Correlations among salivary testosterone, mood, and selective attention to threat in humans. Horm. Behav. 36, 17–24.
- 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.
- 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. Differ. 44, 161–170.