

Women's preferences for masculinity in male faces are predicted by pathogen disgust, but not by moral or sexual disgust

Lisa M. DeBruine^{a,*}, Benedict C. Jones^a, Joshua M. Tybur^b,
Debra Lieberman^c, Vladas Griskevicius^d

^a*School of Psychology, University of Aberdeen, AB24 3FX Aberdeen, Scotland, UK*

^b*Department of Psychology, University of New Mexico, Albuquerque, NM, USA*

^c*Department of Psychology, University of Miami, Miami, FL, USA*

^d*Carlson School of Management, University of Minnesota, Minneapolis, MN, USA*

Initial receipt 21 November 2008; final revision received 3 September 2009

Abstract

Because women's preferences for male masculinity reflect tradeoffs between the benefits of greater genetic health and the costs of lower paternal investment, variables that affect the importance of these costs and benefits also affect masculinity preferences. Concern about disease and pathogens may be one such variable. Here we show that disgust sensitivity in the pathogen domain is positively correlated with facial masculinity preferences, but disgust sensitivity in the moral and sexual domains is not. Our findings present novel evidence that systematic variation in women's preferences for masculine men reflects factors that influence how women resolve the tradeoff between the benefits and costs associated with choosing a masculine partner.

© 2010 Elsevier Inc. All rights reserved.

Keywords: Masculinity; Disgust; Pathogens; Individual differences

Several lines of evidence suggest that masculinity signals genetic (i.e., heritable) good health. For example, facial masculinity in human males is associated with a lower incidence of disease (Rhodes, Chan, Zebrowitz & Simmons, 2003; Thornhill & Gangestad, 2006). Male facial masculinity is also positively correlated with symmetry, a potential signal of developmental stability (Gangestad & Thornhill, 2003; Little, Jones, Waitt et al., 2008). Additionally, women's preferences for masculinity and symmetry are positively correlated, suggesting both traits signal a common underlying quality (Little, Jones, DeBruine & Feinberg, 2008). Although male masculinity is associated with health benefits, it is also associated with negative personality traits and behaviors. For example, high-testosterone men are less likely to marry, more likely to divorce and have more marital problems than lower-testosterone men (Booth & Dabbs, 1993). Men with higher

testosterone are also less likely to feel a need to respond to infant cries than men with lower testosterone (Fleming, Corter, Stallings & Steiner, 2002). Masculine male faces are also ascribed antisocial traits, such as low warmth, low emotionality, dishonesty, low cooperativeness and poor quality as a parent (Boothroyd, Jones, Burt & Perrett, 2007; Perrett et al., 1998). Masculine men are also perceived to have more interest in short-term than in long-term relationships (Kruger, 2006), and masculine men have more short-term, but not long-term, partners than feminine men do (Rhodes, Simmons & Peters, 2005).

Attraction to masculinity is a function of the tradeoffs between the benefits of greater genetic health and the costs of lower investment in relationships and children (Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000; Little, Jones, Penton-Voak, Burt & Perrett, 2002). Factors that affect the relative importance of these costs and benefits affect this tradeoff. For example, the benefits of genetic health for offspring can only be attained when women are able to conceive and preferences for masculine traits are accordingly greater when conception risk is high (for

* Corresponding author.

E-mail address: debruine@abdn.ac.uk (L.M. DeBruine).

reviews, see Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000; Gangestad & Thornhill, 2008; Jones et al., 2008). Additionally, the paternal investment costs associated with partnering with a masculine man are less important in short-term relationships than in long-term relationships. Accordingly, women prefer more masculine men for short-term than for long-term relationships (Burt et al., 2007; Little et al., 2002; Little, Cohen, Jones & Belsky, 2007). Because a partner's heritable health is of greater value when pathogens are a greater concern, concern about pathogens is likely to also be a factor that contributes to the resolution of this tradeoff.

Cross-cultural differences in mate preferences and mating systems vary consistently with differences in pathogen prevalence (Gangestad & Buss, 1993; Low, 1990; Penton-Voak, Jacobson & Trivers, 2004). When people from 29 different cultures were asked to rank a series of attributes based on how important they would be in a mate, people in areas with a high prevalence of pathogens ranked physical attractiveness higher than people in areas with a relatively low prevalence of pathogens did (Gangestad & Buss, 1993). Areas with higher pathogen prevalence also have a higher proportion of polygynous marriages, possibly reflecting that women are trading paternal investment for genetic quality when disease is a greater concern (Low, 1990). Also consistent with these findings, rural Jamaican women prefer masculinity more than British women do, although this may alternatively or additionally be explained by differences in the mating and parenting systems (Penton-Voak et al., 2004). While these studies have emphasized how cross-cultural differences in pathogen levels may affect mate preferences, individual differences in concern about disease and pathogens may also affect mate preferences. Specifically, differences among women in concerns about disease and pathogens may be positively related to preferences for cues of genetic health in potential mates, such as male facial masculinity.

Concern about pathogens can be assessed by measuring disgust sensitivity. Disgust towards potential sources of pathogens has been shown to be a separate domain of the emotion disgust that is relatively independent of the other domains of moral and sexual disgust (Tybur, Lieberman & Griskevicius, 2009). Therefore, we predict that women's preferences for male facial masculinity will be positively associated with their disgust sensitivity in the pathogen domain, but will not necessarily be consistently positively associated with disgust sensitivity in the moral and sexual domains. Such a pattern of results would reveal domain specificity in the relationship between disgust and masculinity preferences and present novel converging evidence that variation in concerns about pathogens and disease influences facultative human mate preferences. We investigated this prediction using two different methods for assessing masculinity preferences: preference for computer graphic-manipulated masculinity (Study 1) and preference for rated masculinity in unmanipulated faces (Study 2).

1. Study 1 — Manipulated masculinity

Computer-graphic methods can be used to objectively and systematically manipulate the masculinity of two-dimensional (2D) face shape (Rowland & Perrett, 1995). This method is widely used in studies of masculinity preferences (e.g., DeBruine et al., 2006; Jones et al., 2005; Penton-Voak et al., 1999; Welling et al., 2007) and yields preferences that are comparable to other methods of manipulating masculinity (DeBruine et al., 2006). Faces manipulated using this method differ reliably in perceived masculinity and dominance (DeBruine et al., 2006; Welling et al., 2007). Additionally, this method produces preferences that correlate with actual and ideal partner masculinity (DeBruine et al., 2006).

A major advantage of the manipulated masculinity method is that it allows masculinity preferences to be assessed independently of other facial characteristics that are correlated with masculinity. For example, masculine male faces are also more symmetric than feminine male faces (Gangestad & Thornhill, 2003; Little, Jones, DeBruine et al., 2008). Masculinity may also correlate with apparent health in unmanipulated faces, but manipulating masculinity does not affect apparent health (Boothroyd et al., 2005).

1.1. Methods

1.1.1. Participants

Participants in Study 1 were 345 women between the ages of 18 and 40 years (mean=25.3, S.D.=6.63). The study was conducted online and participants were recruited by following links from various search engines and listings of online psychology experiments. Previous studies have demonstrated that online and laboratory studies of variation in face preferences produce equivalent patterns of results (e.g., Jones et al., 2005, 2007).

1.1.2. Stimuli

Stimuli were face images of 20 white men (mean=19.5 years, S.D.=2.3) that had been masculinized and feminized using computer-graphic transformation (Rowland & Perrett, 1995) to exaggerate male-typical or female-typical 2D facial configuration. First, male and female prototypes were manufactured by averaging the shapes of 60 white male or 60 white female faces. These prototypes were used to transform the 20 individual face images by adding or subtracting 50% of the linear differences in 2D shape between the male and female prototypes. This process creates masculinized and feminized versions (Fig. 1) of the images that differ in masculinity (i.e., sexual dimorphism) of 2D shape and that are matched in other regards (e.g., skin color; Tiddeman, Burt & Perrett, 2001).

To confirm that this manipulation influenced perceptions of masculinity in the predicted manner, 14 women between the ages of 16 and 40 (mean=23.1, S.D.=7.61) were asked to indicate the more masculine face for each of the 20 pairs of



Fig. 1. Face stimuli from Study 1. The masculinized version is on the left and the feminized version is on the right.

masculinized and feminized faces. The average proportion correct was 95% (S.D.=6.9%; $p < .001$).

1.1.3. Three-Domain Disgust Scale

Participants also completed the Three-Domain Disgust Scale (Tybur et al., 2009). The 21-item measure asks participants to rate each of 21 actions from *not at all disgusting* (0) to *extremely disgusting* (6). The actions were divided into three domains: moral disgust (e.g., deceiving a friend), sexual disgust (e.g., hearing two strangers having sex) and pathogen disgust (e.g., stepping on dog poop). The order of questions was randomized between participants.

To test the factor structure of the Three-Domain Disgust Scale, we first ran a confirmatory factor analysis on the measure using EQS 6.1. The model was constrained so that the seven pathogen items, seven sexual items and seven moral items loaded on separate correlated factors. Model fit was acceptable [χ^2 (186, $N=345$)=342.36, $p < .01$, CFI=.92, RMSEA=.05, SRMR=.06] and was similar to results reported by Tybur et al. (2009). Moral, sexual and pathogen disgust sensitivity were thus each coded as the sum of the ratings (0–6) given to the seven items for each domain. The pathogen, sexual and moral composites demonstrated acceptable internal reliability ($\alpha=.75$, .77 and .86, respectively). The composites were only modestly correlated: the pathogen domain correlated with the sexual and moral domains ($r=.36$ and .15, respectively), and the sexual and moral domains were correlated ($r=.26$).

1.1.4. Procedure

Participants completed a facial masculinity preference test, where they were presented with two versions of the same identity, one masculinized and one feminized, and were asked to choose which face was more attractive. The facial masculinity test comprised 20 face pairs. Order was randomized between participants. Participants also completed the Three-Domain Disgust Scale. The order of questions was randomized between participants. The order of comple-

tion of the facial masculinity preference test and the disgust scale was also randomized between participants.

1.2. Results

Facial masculinity preference scores were coded as the proportion of masculine male faces chosen out of 20, and disgust sensitivity scores were coded as the sum of the seven items for each disgust domain. We analyzed the relationship between facial masculinity preferences and the three domains of disgust sensitivity using linear regression with *facial masculinity preference* as the dependent variable and *pathogen*, *moral* and *sexual* disgust sensitivity as the predictors. The analysis showed a significant effect of pathogen disgust sensitivity ($t=2.30$, $p=.022$, $\beta=.132$), whereby participants with higher sensitivity to disgust in the pathogen domain preferred masculinity more than did those with lower disgust sensitivity. There were no significant effects of moral ($t=-0.01$, $p=.99$, $\beta=-.001$) or sexual ($t=-1.39$, $p=.17$, $\beta=-.082$) disgust sensitivity.

On average, masculinity was preferred on 46% of trials (S.D.=24%) and this was significantly lower than chance ($t_{344}=-2.68$, $p=.008$, $d=0.14$). Additionally, participant age was not correlated with either masculinity preference ($r=.08$, $p=.13$) or pathogen disgust sensitivity ($r=-.08$, $p=.13$).

2. Study 2—Unmanipulated masculinity

Some researchers have suggested that differences among studies in general masculinity preferences for male faces are due to the use of manipulated vs. unmanipulated stimuli (Rennels, Bronstad & Langlois, 2008; see Rhodes, 2006, for a review). Although these studies tend to differ in other regards (e.g., use of rating vs. forced-choice paradigms) and similar variations in findings have also been found among studies using the same methods (see DeBruine et al., 2006 for a review), some researchers suggest that findings using manipulated stimuli should be treated with caution until they are replicated using unmanipulated stimuli (Rennels et al.,

2008; Rhodes, 2006; but see DeBruine, Jones, Smith & Little, 2009). Indeed, changes in masculinity preferences across the menstrual cycle have been replicated with unmanipulated faces (Little, Jones & DeBruine, 2008). In light of these criticisms, in Study 2 we investigated the relationship between pathogen disgust sensitivity and women's preferences for masculinity in unmanipulated male faces. We predict that, as in Study 1, women's preferences for male facial masculinity will be positively correlated with pathogen disgust sensitivity.

2.1. Methods

2.1.1. Participants

Participants were 74 women between the ages of 18 and 40 years (mean=23.8, S.D.=5.38). None of the participants in Study 2 participated in Study 1, which was confirmed by IP address and registration details. As in Study 1, participants were tested online.

2.1.2. Stimuli

Stimuli were the four faces that were rated most masculine and four faces rated most feminine (Fig. 2) from a group of 40 white male faces between the ages of 18 and 25 from the publicly available Productive Aging Laboratory (PAL) database (Minear & Park, 2004). To identify the most and least masculine faces from this sample, the 40 male faces were rated by 25 women between the ages of 17 and 36 years (mean=23.3, S.D.=5.69). Images were rated for masculinity on a scale of 1 (*low*) to 7 (*high*). Inter-rater agreement was high ($\alpha=.87$). The mean masculinity rating of the four least masculine faces was 3.18 (S.D.=0.15) and of the four most masculine faces was 5.24 (S.D.=0.22). A further 21 women between the ages of 16 and 38 years (mean=24.4, S.D.=6.21) were shown all possible pairs of masculine vs. feminine faces (16 trials in total) and were asked to choose the more masculine face in each pair. All women chose the face with higher rated masculinity for all trials ($p<.001$).

2.1.3. Procedure

Participants completed a facial masculinity preference test, where they were presented with two faces of different identities, one from the four most masculine faces and one from the four most feminine faces, and were asked to choose which face was more attractive. The facial masculinity test comprised 16 face pairs; all possible pairings of a masculine face and a feminine face were included. Order was randomized between participants.

As in Study 1, participants also completed the Three-Domain Disgust Scale (Tybur et al., 2009) and the order of completion of the facial masculinity preference test and the disgust scale was randomized between participants.

2.2. Results

Facial masculinity preference scores were coded as the proportion of masculine male faces chosen out of 16. Moral, sexual and pathogen disgust sensitivity were each coded as the sum of the ratings (0–6) given to the seven relevant disgust sensitivity questions.

As in Study 1, we analyzed the relationship between facial masculinity preferences and the three domains of disgust sensitivity using linear regression with *facial masculinity preference* as the dependent variable and *pathogen*, *moral* and *sexual* disgust sensitivity as the predictors. The analysis showed a significant effect of pathogen disgust sensitivity ($t=2.43$, $p=.018$, $\beta=.283$), whereby participants with higher sensitivity to disgust in the pathogen domain preferred masculinity more than did those with lower disgust sensitivity. As in Study 1, we found no significant effects of moral ($t=0.17$, $p=.87$, $\beta=.021$) or sexual ($t=1.44$, $p=.16$, $\beta=.184$) disgust sensitivity.

On average, masculinity was preferred on 80% of trials (S.D.=21%) and this was significantly greater than chance ($t_{73}=12.1$, $p<.001$, $d=1.36$). Additionally, participant age was not correlated with either masculinity preference ($r=.16$, $p=.17$) or pathogen disgust sensitivity ($r=.18$, $p=.13$).



Fig. 2. Face stimuli from Study 2. A face rated as highly masculine is on the left and a face rated as highly feminine is on the right. Faces are from the PAL database (Minear & Park, 2004).

3. Discussion

In both Studies 1 and 2, we found that women's preferences for masculinity in male faces were positively correlated with their disgust sensitivity in the pathogen domain, but not in the moral or sexual domains. Moreover, the relationship between disgust sensitivity in the pathogen domain and masculinity preference was independent of disgust sensitivity in the moral and sexual domains. Thus, our findings for pathogen disgust sensitivity and women's masculinity preference complement previous findings implicating pathogen prevalence in cross-cultural differences in women's mate strategies (Gangestad & Buss, 1993; Low, 1990; Penton-Voak et al., 2004) and present new evidence for the role of pathogen disgust sensitivity in individual differences in masculinity preferences.

Masculinity preferences are known to change across the menstrual cycle (Gangestad, Thornhill & Garver, 2002; Jones et al., 2005; Penton-Voak et al., 1999; Welling et al., 2007). Additionally, concern about pathogens (and, presumably, disgust sensitivity) has been hypothesized to change across the menstrual cycle (Fessler & Navarrete, 2003). Cyclic changes in immunocompetence lead to the prediction that pathogen disgust sensitivity should be greatest when progesterone is high, such as in the mid-luteal phase (Fessler & Navarrete, 2003). Although Fessler and Navarrete (2003) found no evidence for cyclic shifts in pathogen disgust sensitivity, findings from other studies suggest that concerns about pathogens and disease may be influenced by cyclic changes in hormone levels. For example, aversion to facial cues associated with current illness (e.g., pallor) and sensitivity to facial cues of nearby threat (including other-directed disgust expressions) are strongest when progesterone is high (Conway et al., 2007; Jones et al., 2005). However, our results cannot be explained as a byproduct of correlated cyclic shifts in women's heightened pathogen avoidance and preferences for good genes, since shifts toward preferring masculinity occur in the late follicular phase, when progesterone is low (Jones et al., 2005; Puts, 2006), whereas purported shifts in pathogen avoidance occur in the luteal phase. Indeed, since pathogen avoidance and preferences for masculinity should conceivably move in opposite directions across the cycle, participants' cycle status may have attenuated the observed effect. Regardless, this issue can only be elucidated by further investigations of the proximate mechanisms (hormonal or otherwise) influencing sensitivity to pathogen disgust and masculinity preference. Such investigations should be a priority for future research on this topic.

Rennels et al. (2008) recently suggested that findings for systematic variation in masculinity preferences that are observed for judgments of faces in which masculinity of 2D shape was manipulated using computer-graphic methods should be treated with caution until they have been replicated using unmanipulated faces (but see DeBruine et al., 2009, for evidence that their finding was an artifact of uncontrolled

stimuli). It is therefore noteworthy that we observed positive relationships between pathogen disgust sensitivity and masculinity preference using both manipulated and unmanipulated face images. These two methods produced different general preferences, whereby femininity was generally preferred in the manipulated faces and masculinity was generally preferred in the unmanipulated faces (see also Rhodes, 2006). This difference in general masculinity preference underlines that unmanipulated stimuli are likely to confound masculinity and other factors, such as symmetry (Little, Jones, Waite et al., 2008), while manipulated stimuli test preferences for masculinity while holding all other aspects constant. Thus, the slight general preference for the less masculinized face in Study 1 and the strong general preference for the more masculinized face in Study 2 are consistent with previous research and with theory. Despite differences in mean masculinity preference between the studies, identical patterns of systematic variation were observed with both methods. These individual differences, together with identical patterns of cyclic variation for judgments of manipulated faces (Jones et al., 2005; Penton-Voak et al., 1999; Welling et al., 2007) and unmanipulated faces (Little, Jones & DeBruine, 2008), suggest that skepticism of individual differences revealed using manipulated facial masculinity may be unwarranted.

We show that pathogen disgust sensitivity, but not moral or sexual disgust sensitivity, is positively correlated with women's preferences for masculine men. It has been suggested that systematic variation in women's preferences for masculine men reflects factors that influence how women resolve the tradeoff between the benefits and costs associated with choosing a masculine partner (Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000; Little et al., 2002). Our findings present novel, converging evidence for this hypothesis, demonstrating that concern about disease and pathogens biases women's mate preferences toward masculine men.

References

- Booth, A., & Dabbs, J. (1993). Testosterone and men's marriages. *Social Forces*, 72, 463–477.
- Boothroyd, L., Burt, D. M., Cornwell, R. E., Jones, B. C., Little, A. C., & Tiddeman, B. P., et al. (2005). Facial masculinity is related to perceived age but not perceived health. *Evolution and Human Behavior*, 26, 417–431 (DOI 10.1016/j.evolhumbehav.2005.01.001).
- Boothroyd, L. G., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Partner characteristics associated with masculinity, health and maturity in male faces. *Personality and Individual Differences*, 43, 1161–1173 (DOI 10.1016/j.paid.2007.03.008).
- Burt, D. M., Kenridge, R. W., Good, J. M. M., Perrett, D. I., Tiddeman, B. P., & Boothroyd, L. G. (2007). Q-cgi: New techniques to assess variation in perception applied to facial attractiveness. *Proceedings of the Royal Society of London B*, 274, 2779–2784 (DOI 10.1098/rspb.2007.1037).
- Conway, C. A., Jones, B. C., DeBruine, L. M., Welling, L. L., Law Smith, M., & Perrett, D. I., et al. (2007). Salience of emotional displays of danger and contagion in faces is enhanced when progesterone levels are raised. *Hormones and Behavior*, 51, 202–206.

- DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., & Penton-Voak, I. S., et al. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society of London B*, 273, 1355–1360 (DOI 10.1098/rspb.2005.3445).
- DeBruine, L. M., Jones, B. C., Smith, F. G., & Little, A. C. (2009). Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, in press.
- Fessler, D. M. T., & Navarrete, C. D. (2003). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior*, 24(6), 406–417 (DOI 10.1016/S1090-5138(03)00054-0).
- Fink, B., & Penton-Voak, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science*, 11, 154–158.
- Fleming, A. S., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*, 42(4), 399–413 (DOI 10.1006/hbeh.2002.1840).
- Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, 14, 89–96 (DOI 10.1016/0162-3095(93)90009-7).
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23, 573–644.
- Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior*, 24, 231–241 (DOI 10.1016/S1090-5138(03)00017-5).
- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society of London B*, 275, 991–1000.
- Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate-retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London B*, 269(1494), 975–982 (DOI 10.1098/rspb.2001.1952).
- 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. *Evolution and Human Behavior*, 28, 439–446 (DOI 10.1016/j.evolhumbehav.2007.07.006).
- 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. *Archives of Sexual Behavior*, 37(1), 78–84 (DOI 10.1007/s10508-007-9268-y).
- Jones, B. C., Little, A. C., Boothroyd, L. G., DeBruine, L. M., Feinberg, D. R., & Law Smith, M. J., et al. (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. *Hormones and Behavior*, 48, 283–290 (DOI 10.1016/j.yhbeh.2005.03.010).
- Kruger, D. J. (2006). Male facial masculinity influences attributions of personality and reproductive strategy. *Personal Relationships*, 13(4), 451–463 (DOI 10.1111/j.1475-6811.2006.00129.x).
- Little, A. C., Cohen, D. L., Jones, B. C., & Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. *Behavioral Ecology and Sociobiology*, 61(6), 967–973 (DOI 10.1007/s00265-006-0325-7).
- Little, A. C., Jones, B. C., & DeBruine, L. M. (2008). Preferences for variation in masculinity in real male faces change across the menstrual cycle. *Personality and Individual Differences*, 45(6), 478–482 (DOI 10.1016/j.paid.2008.05.024).
- Little, A. C., Jones, B. C., DeBruine, L. M., & Feinberg, D. R. (2008). Symmetry and sexual-dimorphism in human faces: Interrelated preferences suggest both signal quality. *Behavioral Ecology*, 19(4), 902–908 (DOI 10.1093/beheco/arn049).
- Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London B*, 269(1496), 1095–1103 (DOI 10.1098/rspb.2002.1984).
- Little, A. C., Jones, B. C., Waitt, C., Tiddeman, B. P., Feinberg, D. R., & Perrett, D. I., et al. (2008). Symmetry is related to sexual dimorphism in faces: Data across culture and species. *PLoS One*, 3(5), 2106 (DOI 10.1371/journal.pone.0002106).
- Low, B. (1990). Marriage systems and pathogen stress in human societies. *American Zoologist*, 30, 325–339.
- Minear, M., & Park, D. C. (2004). A lifespan database of adult facial stimuli. *Behavior Research Methods, Instruments, & Computers*, 36(4), 630–633.
- Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgements of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior*, 25, 355–370 (DOI 10.1016/j.evolhumbehav.2004.06.002).
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., & Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741–742.
- Perrett, D. I., Lee, K., Penton-Voak, I. S., Rowland, D., Yoshikawa, S., & Burt, D. M., et al. (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 Nature*, 17, 114–127.
- Rennels, J. L., Bronstad, P. M., & Langlois, J. H. (2008). Are attractive men's faces masculine or feminine? The importance of type of facial stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, 34(4), 884–893 (DOI 10.1037/0096-1523.34.4.884).
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, 57, 199–226 (DOI 10.1146/annurev.psych.57.102904.190208).
- Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London B*, 270(S1), S93–S95 (DOI 10.1098/rsbl.2003.0023).
- Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behaviour: Does attractiveness enhance mating success? *Evolution and Human Behavior*, 26, 186–201 (DOI 10.1016/j.evolhumbehav.2004.08.014).
- Rowland, D., & Perrett, D. I. (1995). Manipulating facial appearance through shape and color. *IEEE Computer Graphics and Applications*, 15, 70–76.
- Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, 27, 131–144.
- Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications*, 1, 42–50.
- Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology*, 97, 103–122 (DOI 10.1037/a0015474).
- Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., & Little, A. C., et al. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones and Behavior*, 52, 156–161 (DOI 10.1016/j.yhbeh.2007.01.010).