

Preferences for masculinity in male bodies change across the menstrual cycle

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Abstract

In human females cyclic shifts in preference have been documented for odour and physical and behavioral male traits. Women prefer the smell of dominant males, more masculine male faces and men behaving more dominantly when at peak fertility than at other times in their menstrual cycle. Here we examine variation in preferences for body sexual dimorphism. Across two studies, both between- and within-participant, we show that women prefer greater masculinity in male bodies at times when their fertility is likely highest, in the follicular phase of their cycle. Shifts were seen when rating for a short-term but not when rating for a long-term relationship. In line with studies showing similar effects for facial sexual dimorphism, we also show that women prefer greater masculinity when they think themselves attractive than when they think themselves less attractive. These results indicate that women's preferences for sexual dimorphism in male bodies follow a similar pattern as found for sexual dimorphism and dominance in other domains and such differences in preference may serve a similar function. Cyclic preferences could influence women to select partners when most likely to become pregnant that possess traits that may be most likely to maximize their offspring's quality via attraction to masculinity or serve to help acquire investment via attraction to femininity.

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Many studies have demonstrated that women's preferences for male traits change across the menstrual cycle. Increased preferences for facial masculinity (Frost, 1994; Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999), vocal masculinity (Feinberg et al., 2006; Puts, 2005), videoclips of dominant behavior (Gangestad et al., 2004) and for taller men (Pawlowski and Jasienska, 2005) that coincide with the late follicular (i.e., fertile) menstrual cycle phase have been reported. These changes in preferences for masculine men are potentially adaptive. Human males bring two factors to a parenting relationship: investment in their partners and offspring and potential heritable benefits (e.g., genes for high-quality immune systems). Masculinity in males has long been thought to be indicator of quality via classic handicap models (Folstad and Karter, 1992); as testosterone handicaps the immune system (Kanda et al., 1996) and therefore only high-

quality males can afford to be masculine (Thornhill and Gangestad, 1999). The relationship between masculinity and quality is controversial and there are several lines of reason involved in why it is preferred (Getty, 2002; Thornhill and Gangestad, 1999).

While masculine faced men are healthier than their feminine faced counterparts (Rhodes et al., 2003), masculinity in a partner also carries a cost. Men with masculine faces have higher circulating testosterone levels (Penton-Voak and Chen, 2004), which are linked to marital instability and lower levels of attachment in relationships (Booth and Dabbs, 1993; Burnham et al., 2003). Thus, variation in preferences during the menstrual cycle may enable women to maximize the benefits of their mate preferences, potentially shifting priorities between heritable benefits to offspring and investment (Penton-Voak et al., 1999).

Although peaks in sexual desire and activity have been reported at different stages across the menstrual cycle (Regan, 1996), studies have reported that women with partners may be more likely to engage in extra-pair sex at peak fertility. Extra-pair copulation is 2.5 times more likely during the follicular

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phase than in the luteal phase (Baker and Bellis, 1995). Further evidence for possible extra-pair behavior comes from studies showing that women at peak fertility are more likely to have sexual fantasies about men other than their primary partner (Gangestad et al., 2002), express a greater interest in attending social gatherings where they might meet men at peak fertility (Haselton and Gangestad, 2006) and to report being more committed to their partners during the luteal phase of the menstrual cycle and less committed in the late follicular phase (Jones et al., 2005). These studies suggest a possible mechanism whereby women may maximize their chances of becoming pregnant with the offspring of males chosen for extra-pair affairs. Such males may be selected for possessing superior or alternative genes to the woman's current partner.

As an alternative, or perhaps complementary, explanation for shifting preferences, findings demonstrating the role of changes in progesterone level for increased commitment to partners and increased preferences for both feminine faced men and women during the luteal phase of the menstrual cycle may increase the care and support that is available during hormonal profiles similar to those that characterize pregnancy (Jones et al., 2005). In this way, rather than acquiring direct benefits for offspring from masculine men, women instead maximize investment from feminine men (Jones et al., 2005).

Preferences for masculinity in faces have also been found to be moderated by other factors relating to potentially strategic choice. Condition-dependent mate choice is seen in female fish species (Bakker et al., 1999) and humans (Little et al., 2001; Penton-Voak et al., 2003). Attractive women, possibly due to their increased competitiveness for mates, are more discriminating than less attractive women, displaying greater preferences for masculinity in faces (Little et al., 2001; Penton-Voak et al., 2003). For short-term relationships, women are more likely to choose an attractive male who is less cooperative and appears to have poorer parenting qualities over a less attractive male who is more cooperative and with better parenting qualities (Scheib, 2001). By contrast, for long-term contexts women may choose the less attractive but more cooperative man more often (Scheib, 2001). In face preference tasks, women judging for short-term relationships prefer more masculinity in faces than those judging for long-term relationships (Little et al., 2002). Women also prefer to select taller partners for short-term than for long-term relationships (Pawlowski and Jasienska, 2005). It is possible that some women may choose a long-term partner whose feminine appearance suggests cooperation and extended paternal care and/or choose short-term partners whose higher facial masculinity may indicate better genetic quality (Little et al., 2002; Perrett et al., 1998). Already having a partner has also been shown to predict female face preferences. An increased preference for genetic fitness over signs of parental investment would be expected in extra-pair copulations when a woman has already acquired a long-term partner. Indeed, Little et al. (2002) have shown that women who have partners prefer masculinity in faces more than those without a partner.

Given the many effects of menstrual cycle on masculinity preferences, the current study examined preferences for sexual dimorphism in body shape across the cycle. Preferences for

male body shape have generally used line drawings which have manipulated specific aspects of shape. Such studies have revealed preferences for broad shoulders (Dixson et al., 2003), taller men, particularly at high fertility (Pawlowski and Jasienska, 2005), masculine (low) waist to chest ratios, broad shoulders relative to small waist (Maisey et al., 1999) and masculine (high) waist to hip ratios (WHR) (Dixson et al., 2003; Singh, 1995). WHR is sexually dimorphic, with women tending towards a lower ratio during their fertile years that typifies the hourglass figure. Men tend to have more similar waist and hip measurements, resulting in a less curvy appearance. This occurs because testosterone stimulates fat deposits in the abdominal region while inhibiting fat deposits in the buttocks and thighs (Rebuffescribe, 1987). The current study uses realistic male images manipulated with computer graphic techniques for global sexual dimorphism using methods adapted from those used in many studies of preferences for masculinity in faces (Little et al., 2001; Little and Hancock, 2002; Little et al., 2002; Penton-Voak et al., 1999; Perrett et al., 1998). By using the difference between male and female bodies, the resulting images differ in the average way that men differ from women in shape and encompass general aspects of masculine shape (controlling for height differences). The current study focused on whether preferences for sexual dimorphism in shape change across the menstrual cycle following studies demonstrating that preferences for masculinity in face shape and height also change. We also examine other variables known to influence preferences for masculinity in faces: temporal context (short vs. long term), partnership status and condition-dependent preferences. For condition-dependent preferences we used self-perceived attractiveness as a proxy for mate-value/condition following previous studies (Little et al., 2001).

We predicted, following similar results for preferences for masculinity in male faces, that women would prefer more masculine male bodies when in the follicular phase of their cycle and that preferences for masculinity would be enhanced for short-term relationships. We also predicted that menstrual cycle shifts may be greater for short-term relationships, again following findings from face preferences. In Study 1 where we examined self-perceived attractiveness we expected that women viewing themselves as more attractive would have enhanced preferences for masculinity. We also included a separate analysis of women who reported using hormonal contraception. These participants represent a control group and were not expected to show menstrual cycle shifts in preference.

Methods

Study 1

Participants

Ninety-seven female participants (aged 17–35, mean age=24.9, SD=5.5) took part in the study. The study was administered over the internet via a link from www.alittlelab.com and participants were volunteers selected for reporting to be heterosexual, not using oral or other hormonal contraception, being between 17 and 35 years of age, not being pregnant and having a restricted range in their reported cycle date (days since menstruating reported as 0–28, 61 were classified low fertile and 36 high fertile, see classification below). Sixty-one women (aged 17–35, mean age=24.9, SD=5.4) who reported using hormonal

contraception but otherwise fulfilled the above criteria also took part in the study (37 were classified low fertile and 24 high fertile. While those using oral contraception do not differ in conception risk across the cycle, the same terminology is used here for comparative purposes).

Conception risk

Following previous studies of preferences (Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), we used a standard 28-day model of the female menstrual cycle to divide women into high (days 6–14) and low (days 0–5 and 15–28) conception risk based on self-reports of the previous onset of menses. These groups correspond to the follicular phase and menses and the luteal phase respectively (e.g., Regan, 1996). The mean days since menstruation for the fertile grouping was 10.0 (SD=2.7). For the less fertile grouping, 11 women reported days 0–5 (mean=2.3, SD=1.8) and 31 women reported days 15–28 (mean=20.6, SD=4.5). To check whether our split captured differences in fertility we calculated conception risk for each individual based on their reported menstruation (counting from onset of previous menses) by using values reported in Wilcox et al. (2001). Wilcox et al. provide likelihood of conception from a single act of intercourse for each day of the menstrual cycle based on a study of 221 women who were attempting to conceive. The highest probability from this data is only 0.086. An independent samples *t*-test revealed our high fertility group (mean=0.053, SD=0.027) was predicted to have a higher conception risk than our low fertility group (mean=0.017, SD=0.023, $t_{95}=6.8$, $p<0.001$).

Stimuli

Ten pairs of body images were constructed from 10 individual photographs of male and female bodies. For every image 52 feature points were delineated on each body image from which the average male and female shapes were calculated. Composite images were created by warping, and then superimposing all of the male or female bodies into each of the average body shapes. The images were made perfectly symmetrical by combining them with their mirror image prior to masculinity manipulation and were equalized in height based on the highest and lowest points. Fig. 1A shows the composite images used to define the vector and the points used to define body shape. Using the linear difference between feature points in the average male and female shape each male body was transformed both +50% masculinized and +50% feminized to create a pair differing in masculine shape only. Fig. 1B shows an example of a masculinized and feminized male composite body (individual images were used in the test but are not presented here). These techniques have been used in the manipulation of facial masculinity and other face traits (Benson and Perrett, 1993; Little and Hancock, 2002; Perrett et al., 1998; Tiddeman et al., 2001).

Procedure

Participants were presented with 10 forced-choice paired image trials (choosing between a masculinized and feminized version of the same body) for each term (long and short) followed by an on-screen questionnaire. The trials were presented in random order with the side each body is presented on also randomized and with participants being cued to make judgments based on either short- or long-term relationships by the message “choose the body you think is most attractive for a short [or long] term relationship.” Definitions of short- and long-term relationships were provided prior to rating for each condition.

Short-term. You are looking for the type of person who would be attractive in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship and possibility of a one-night stand.

Long-term. You are looking for the type of person who would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with and someone you may, at some point, wish to marry (or enter into a relationship on similar grounds as marriage).

These definitions were presented to encourage participants to think about the general issues in partnership choice by term and are not presented here as strict definitions of relationship type.

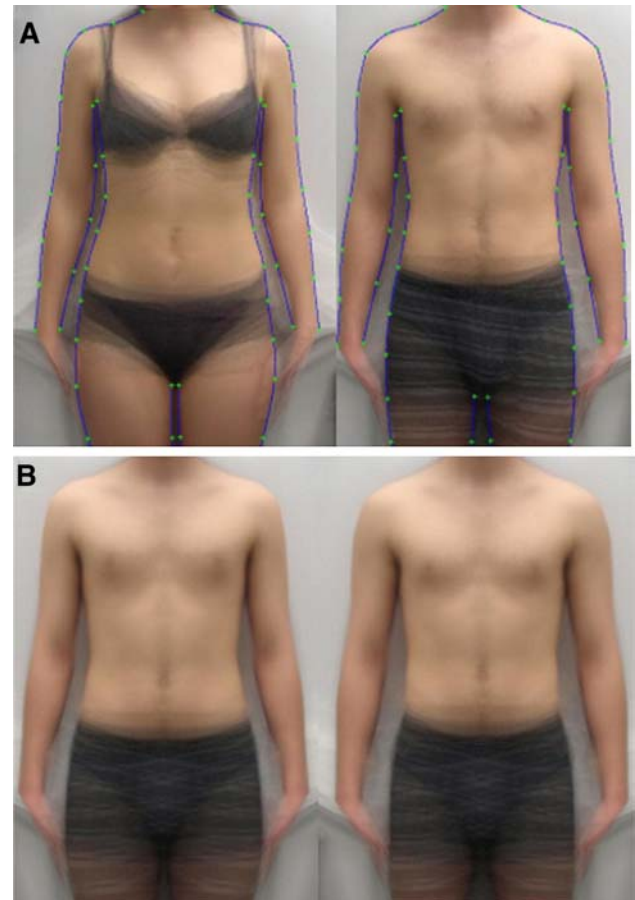


Fig. 1. Composite female and male body images (A). Examples of feminized (left) and masculinized (right) male bodies (B). These images are composite bodies and represent the transform applied to individual body images and not the individual images used in the study.

Participants rated both for long- and short-term relationships and order of rating by term was randomized. Prior to ratings, a questionnaire was administered. Participant attractiveness was measured by giving participants a seven-point scale upon which to rate themselves (1=low, 4=average, 7=high). Other questions, age, partner (yes/no) and sexuality, were presented in the same questionnaire.

Proportion of masculine bodies chosen was calculated for each participant by taking the number of masculine bodies picked from the pairs (from 0 to 10 out of the 10 pairs) and multiplying by 100 to represent a percentage.

Results

A one-sample *t*-test against no preference (50%, no preference) revealed that women preferred more masculine male bodies for both long-term (mean=74.4%, SD=18.7, $t_{96}=12.9$, $p<0.001$) and short-term relationships (mean=73.4%, SD=18.3, $t_{96}=12.6$, $p<0.001$).

A repeated measures ANOVA with term (long/short) as a within-participant factor, partnership status and fertility as between-participant factors, and age and self-rated attractiveness entered as covariates was conducted. This revealed a close to significant interaction between term and fertility ($F_{1,91}=3.9$, $p=0.053$). We note that as we predict this relationship, this is conventionally significant using a one-tailed probability (0.027).

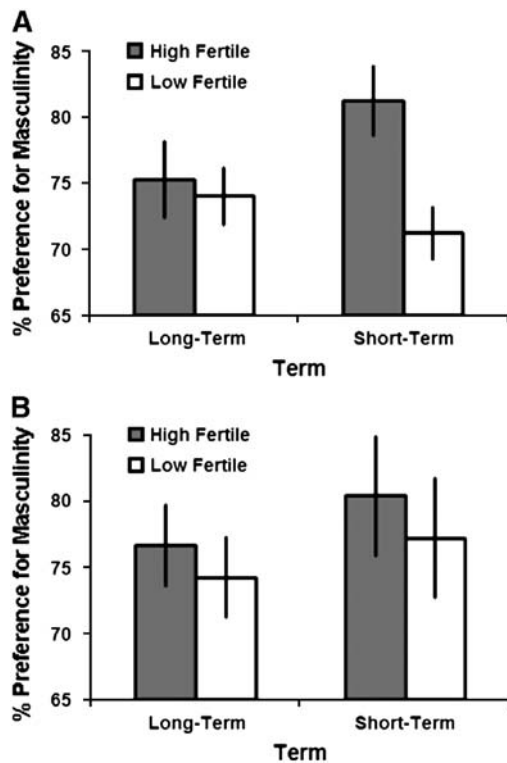


Fig. 2. Percentage of preferences for masculinity (± 1 SE of mean) in Study 1 for long- and short-term judgments by fertility (high/low) for those not using hormonal contraception (A) and those using hormonal contraception (B). A repeated measures ANOVA with term as a within-participant factor and fertility as a between-participant (high $N=36$ /low $N=61$) factor revealed a significant interaction between term and fertility (one-tailed test, $F_{1,91}=3.9$, $p=0.027$). See main text for other factors and covariates in this analysis.

The interaction between fertility and term can be seen in Fig. 2 and indicates that women prefer more masculine bodies at high fertility than at low fertility for short-term but not long-term relationships. In between-participant factors, there were significant effects of age ($F_{1,91}=12.0$, $p<0.001$), self-rated attractiveness ($F_{1,91}=6.2$, $p=0.014$) and fertility ($F_{1,91}=8.0$, $p=0.006$). The main effect of fertility reflected a general tendency for women to prefer more masculine bodies at high fertility (Fig. 2). No other effects or interactions were significant (all $F<1.9$, $p>0.18$).

Following up the main effects of age and self rated attractiveness in the non-hormonal contraceptive group, we conducted Pearson product moment correlations. This revealed significant positive correlations between age and preferences for masculinity in male bodies for short-term relationships ($r=0.22$, $p=0.029$) and between self-rated attractiveness and preferences for masculinity in male bodies for long-term relationships ($r=0.21$, $p=0.041$). While not significant, positive correlations were also found for age for long-term ($r=0.18$, $p=0.076$) and self-rated attractiveness for short-term ($r=0.16$, $p=0.12$) relationships. We note the lack of interaction above indicates that both variables should be treated as positively related to preference irrespective of term.

For those reporting oral/hormonal contraception use we again found preferences for masculinity for both long-term (mean=75.7%, $SD=14.2$, $t_{60}=14.2$, $p<0.001$) and short-term

(mean=79.8%, $SD=17.9$, $t_{60}=13.0$, $p<0.001$) judgments. Repeating the above ANOVA, however, revealed no significant effects or interactions (all $F<2.3$, $p>0.14$), including no main effect of fertility ($F_{1,55}=0.35$, $p=0.85$) and no interaction between fertility and term ($F_{1,55}=0.10$, $p=0.92$).

Study 2

Participants

Seventeen female participants (aged 18–31, mean age=22.9, $SD=3.4$) took part in the study. The study was administered in the laboratory and participants were volunteers who were paid £5 for participation and were selected for reporting to be heterosexual and not using oral or other hormonal contraception. Participants were recruited via an advert on an online poster system which specified that the study concerned the female menstrual cycle and that participants would be tested on two separate occasions. Eight additional individuals were excluded from the study due to their failing to return for the second testing session, providing incomplete menstrual cycle information in one of the sessions or falling into the same fertility grouping at both testing sessions (see below).

Stimuli

The same stimuli as used in Study 1 were used in Study 2.

Procedure

The procedure for Study 2 was identical to that of Study 1, though it was carried out in a laboratory. Participants were tested twice, once in the late follicular phase of the menstrual cycle (days 6–14) and once outside this phase. Participants were not asked to report for their first session during a particular fertility phase, and second sessions were scheduled to fall during the opposite phase. Nine individuals participated in their first session when in the high fertile phase and eight individuals participated in their first session when in the low fertile phase.

Conception risk

Conception risk was calculated as outlined in Study 1. Here participants were asked to provide the date of onset of their previous or current menses in both testing sessions. One of the experimenters used this date to calculate a second testing session falling into high or low fertile period depending on their initial grouping. The mean days since menstruation for the fertile grouping was 10.2 ($SD=2.9$). For the less fertile grouping, 5 women reported days 0–5 (mean=4.2, $SD=0.8$) and 12 women reported days 15–28 (mean=21.6, $SD=5.5$). Following our analysis of fertility differences based on conception risk above, an independent samples t -test again revealed that our high fertility group (mean=0.055, $SD=0.029$) was predicted to have a higher conception risk than our low fertility group (mean=0.019, $SD=0.014$, $t_{32}=4.6$, $p<0.001$).

Results

A repeated measures ANOVA with fertility (high/low) and term (long/short) as within-participant factors revealed no

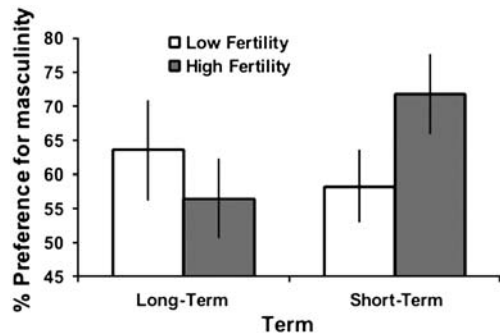


Fig. 3. Percentage of preferences for masculinity (± 1 SE of mean) in Study 2 for long- and short-term judgments by fertility (high/low). A repeated measures ANOVA with fertility and term as within-participant factors revealed a significant interaction between fertility and term ($N=17$, $F_{1,16}=7.3$, $p=0.016$).

significant main effects of either fertility ($F_{1,16}=0.8$, $p=0.37$) or term ($F_{1,16}=1.8$, $p=0.20$) and a significant interaction between fertility and term ($F_{1,16}=7.3$, $p=0.016$). The interaction indicated that women most preferred masculinity in male bodies when rating for a short-term relationship at high fertility, as shown in Fig. 3. The smaller number of participants here meant that while data was collected, effects of partnership status and self-perceived attractiveness were not analysed in Study 2.

Adding order of testing (whether individuals were in the high or low fertility group at the first testing session) as a between-participant variable revealed that order did not interact with preferences (all F involving order < 2.6 , $p > 0.13$).

Discussion

The current study demonstrates that female preferences for masculinity in male bodies change across the menstrual cycle and in relation to other variables known to influence preferences for masculinity in face shape. Women preferred more masculine male body shapes when they were in the late follicular, fertile phase of the menstrual cycle though this effect was seen mainly for choices of short-term partner. As in previous studies, individuals reporting hormonal contraceptive use did not show cyclic shifts in preference. Women also preferred more masculine body shapes if they thought themselves more attractive, and overall women found masculine body shape more attractive than feminine shape.

Between-participant data are not ideal to study a within-participant effect and our within-participant sample is small, but together our data demonstrate that menstrual cycle effects on preferences for masculinity in bodies can be found in both types of study. There are also several different methods for dividing participants according to their cycle, and here we show using one common method of classification based on allocation to groups that menstrual cycle effects on body preferences can be found. We note that any errors in the allocation to group, such as inaccurate reporting from the participants, would be most likely to decrease the chance of finding a significant effect.

The observed change in preferences for masculine male body shapes during the menstrual cycle is in line with previous work demonstrating increased preferences for vocal masculinity (Feinberg et al., 2006; Puts, 2005) and dominant behavior (Gangestad et al., 2004) at peak fertility. The results of the current study are most akin to studies examining menstrual cycle effects on preferences for facial masculinity (Frost, 1994; Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999) and for height (Pawlowski and Jasienska, 2005) as here we also examine visual cues based on physical shape. Our images use the same methodology to define sexual dimorphism as that used in some studies of face preference and address different aspects of masculinity in bodies to those examined in previous studies, examining shape, not height, and using realistic individual male body images. We note that masculinity change in our images used all of the differences in shape between male and female bodies. Future studies may usefully parse the different traits that drive shifting preferences for masculinity in bodies.

Women preferred masculine bodies at peak fertility particularly for short-term relationships, and this suggests that body masculinity may be more highly valued under circumstances where the potential to pass traits to offspring is high and where parental investment is relatively unimportant. As women have sexual fantasies about men other than their partners (Gangestad et al., 2002) and are less committed to their partners (Jones et al., 2005) at peak fertility, women may maximize their chances of becoming pregnant with the offspring of males chosen for extra-pair affairs, though we note that we found no interaction with partnership status for these variables. Functionally, shifting preferences may then lead to maximising the likelihood that offspring inherit strong immune systems via good genes from fathers (Penton-Voak and Perrett, 2000) or promote strategies to associate with more investing individuals when not at peak fertility (Jones et al., 2005). Of course, a mechanism that maximizes good gene benefits from extra-pair partners may also serve to maximize genetic benefits in offspring for women without partners.

Previous studies have revealed preferences for broad shoulders (Dixon et al., 2003), taller men, particularly at high fertility (Pawlowski and Jasienska, 2005) and masculine waist to hip ratios (WHR) (Dixon et al., 2003; Singh, 1995); these results are supported by those of the current study in which we have used photorealistic individual images of bodies. There are potential benefits to offspring in females' mating with males who have masculine body shapes. Within women at least, typical female WHR is associated with higher levels of circulating oestrogen, whereas higher WHR is associated with higher levels of circulating testosterone (Evans et al., 1983). Women may then be choosing men with higher testosterone at peak fertility and for short-term relationships. Masculine-bodied males may also have physical advantages leading them to be dominant over more feminine-bodied men. Any or all of these factors may lead to the general preference for masculine bodies and to the increased attraction to body shape masculinity at peak fertility and when rating for short-term partners. If this is so, it is interesting to consider why masculinity is not preferred at all times and in all contexts. To echo arguments put forward in the facial

masculinity literature, masculine-bodied men appear to be valued and this may lead them to invest less in relationships because they can more easily secure matings (Gangestad and Simpson, 2000). As masculine body shape may be related to testosterone (Rebuffescrive, 1987), there is a putative link to lower levels of commitment (Booth and Dabbs, 1993; Burnham et al., 2003).

Self-rated attractiveness was positively related to masculinity preference in Study 1 for both long- and short-term ratings, with effects being significant only for long-term judgments (though we note that we found no interaction for term). A similar effect has been demonstrated for facial masculinity preferences (Little et al., 2001). Explanations for findings for faces have focused on female competitiveness to maintain long-term relationships with masculine men and the results here suggest that attractive women may also be more competitive when it comes to attracting and maintaining relationships with masculine-bodied men.

In summary, the current studies suggest that the menstrual cycle has an important impact on body preferences, with women preferring more masculine body shapes at peak fertility. We suggest that ideas of evolved mechanisms promoting attention to relevant traits at peak fertility may provide a parsimonious explanation for the observed results.

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References

- Baker, R.R., Bellis, M.A., 1995. *Human Sperm Competition: Copulation, Masturbation and Infidelity*. Chapman and Hall, London.
- Bakker, T.C.M., Künzler, R., Mazzi, D., 1999. Condition-related mate-choice in sticklebacks. *Nature* 401, 234.
- Benson, P.J., Perrett, D.I., 1993. Extracting prototypical facial images from exemplars. *Perception* 22, 257–262.
- Booth, A., Dabbs, J., 1993. Testosterone and men's marriages. *Soc. Forces* 72, 463–477.
- Burnham, T.C., Chapman, J.F., Gray, P.B., McIntyre, M.H., Lipson, S.F., Ellison, P.T., 2003. Men in committed, romantic relationships have lower testosterone. *Horm. Behav.* 44 (2), 119–122.
- Dixon, A.F., Halliwell, G., East, R., Wignarajah, P., Anderson, M.J., 2003. Masculine somatotype and hirsuteness as determinants of sexual attractiveness to women. *Arch. Sex. Behav.* 32 (1), 29–39.
- Evans, D.J., Hoffmann, R.G., Kalkhoff, R.K., Kissebah, A.H., 1983. Relationship of androgenic activity to body-fat topography, fat-cell morphology, and metabolic aberrations in premenopausal women. *J. Clin. Endocrinol. Metab.* 57 (2), 304–310.
- 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 (2), 215–222.
- Folstad, I., Karter, A.J., 1992. Parasites, bright males and the immunocompetence handicap. *Am. Nat.* 139, 603–622.
- Frost, P., 1994. Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. *Percept. Mot. Skills* 79, 507–514.
- Gangestad, S.W., Simpson, J.A., 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain Sci.* 23, 573–644.
- 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 Series B-Biological Sciences*, vol. 269, pp. 975–982.
- Gangestad, S.W., Simpson, J.A., Cousins, A.J., Garver-Apgar, C.E., Christensen, N.P., 2004. Women's preferences for male behavioral displays change across the menstrual cycle. *Psychol. Sci.* 15 (3), 203–207.
- Getty, T., 2002. Signaling health versus parasites. *Am. Nat.* 159 (4), 363–371.
- Haselton, M.G., Gangestad, S.W., 2006. Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Horm. Behav.* 49 (4), 509–518.
- 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 (3), 283–290.
- Kanda, N., Tsuchida, T., Tamaki, K., 1996. Testosterone inhibits immunoglobulin production by human peripheral blood mononuclear cells. *Clin. Exp. Immunol.* 106, 410–415.
- Little, A.C., Hancock, P.J.B., 2002. The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *Br. J. Psychol.* 93, 451–464.
- Little, A.C., Burt, D.M., Penton-Voak, I.S., Perrett, D.I., 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. London, B* 268, 39–44.
- Little, A.C., Jones, B.C., Penton-Voak, I.S., Burt, D.M., Perrett, D.I., 2002. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc. R. Soc. London, B* 269, 1095–1100.
- Maisey, D.S., Vale, E.L.E., Cornelissen, P.L., Tovee, M.J., 1999. Characteristics of male attractiveness for women. *Lancet* 353 (9163), 1500.
- Pawlowski, B., Jasienska, G., 2005. Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biol. Psychol.* 70 (1), 38–43.
- 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.
- 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.
- 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.
- 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., 2005. Mating context and menstrual phase affect women's preferences for male voice pitch. *Evol. Hum. Behav.* 26 (5), 388–397.
- Rebuffescrive, M., 1987. Regional adipose-tissue metabolism in men and in women during menstrual-cycle, pregnancy, lactation, and menopause. *Int. J. Obes.* 11, 1.
- Regan, P.C., 1996. Rhythms of desire: the association between menstrual cycle phases and female sexual desire. *Can. J. Hum. Sex.* 5 (3), 145–156.
- Rhodes, G., Chan, J., Zebrowitz, L.A., Simmons, L.W., 2003. Does sexual dimorphism in human faces signal health? *Proc. R. Soc. London Ser. B, Biol. Sci.* 270, S93–S95.

- Scheib, J.E., 2001. Context-specific mate choice criteria: women's trade-offs in the contexts of long-term and extra-pair mateships. *Pers. Relatsh.* 8, 371–389.
- Singh, D., 1995. Female judgment of male attractiveness and desirability for relationships—Role of waist-to-hip ratio and financial status. *J. Person. Soc. Psychol.* 69 (6), 1089–1101.
- Thornhill, R., Gangestad, S.W., 1999. Facial attractiveness. *Trends Cogn. Sci.* 3 (12), 452–460.
- Tiddeman, B.P., Burt, D.M., Perrett, D.I., 2001. Prototyping and transforming facial texture for perception research. *IEEE Comput. Graph. Appl.* 21, 42–50.
- Wilcox, A.J., Dunson, D.B., Weinberg, C.R., Trussell, J., Baird, D.D., 2001. Likelihood of conception with a single act of intercourse: providing benchmark rates for assessment of post-coital contraceptives. *Contraception* 63 (4), 211–215.