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Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context

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Summary In women, changes in preference during the menstrual cycle have been documented for attractiveness judgements of odour and various physical and behavioural male traits. Although many studies have demonstrated greater attraction to masculine traits, such as male faces, bodies, and voices, at high fertility, several recent studies present null results for these shifts in preferences. Moreover, evidence for stronger attraction to symmetric faces at high fertility is equivocal. Here we examined variation in preferences across the cycle for both facial masculinity and symmetry according to relationship context. Using both within-subject (Study 1) and between-subject (Study2) designs, we show that women prefer masculinity and symmetry in male faces at times when their fertility is likely to be highest (during the follicular phase of their cycle) when judging the faces for short-term relationship attractiveness. No effect of cycle was seen for long-term judgements. These results indicate that cyclic shifts in women are most apparent when judging for short-term relationships, which may explain the null results in studies where only general attractiveness was assessed. Cyclical preferences could influence women to select a partner who possesses traits that may enhance her offspring's quality at times when conception is most likely and/or serve to improve partner investment when investment is important.

1. Introduction

Women differ in their face preferences and one biological explanation for within-individual variation lies with hormonal changes during the menstrual cycle. Many studies have demonstrated that women's preferences for certain male traits change during the menstrual cycle. Increased preferences for facial masculinity (Frost, 1994; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Johnston et al., 2001), vocal masculinity (Puts, 2005; Feinberg et al., 2006), dominant behaviour (Gangestad et al., 2004), the smell of dominant men (Havlicek et al., 2005) and for masculine body shapes (Little et al., 2007b) that coincide with the late follicular (i.e. fertile) menstrual cycle phase have been

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reported. Cyclic shifts are also seen for other mate choice relevant traits whereby fertile women are quicker to categorise men's faces as male (Macrae et al., 2002) and generally rate men as more attractive (Danel and Pawlowski, 2006). Shifts are also seen for face traits such as self-resemblance (DeBruine et al., 2005) and are also evident in increases in pupil diameter when viewing sexually partners during the fertile phase (Laeng and Falkenberg, 2007). Cyclic shifts are thought to reflect the underlying effects of female hormones on preferences for male traits. Several hormones change across the cycle and shifts have been linked to oestrogen (Roney and Simmons, 2008), progesterone (Jones et al., 2005; Puts, 2005), and testosterone (Welling et al., 2007), although such shifts are potentially best explained by complex interactions among multiple hormones (Feinberg et al., 2006; Welling et al., 2007).

Changes in preferences for masculine men are potentially adaptive. Two of the factors that human males bring to a parenting relationship (investment in their partner and offspring, and potential heritable benefits) have been the focus of most research. Masculinity in males has long been thought to be indicator of quality via classic handicap models (Folstad and Karter, 1992); as higher testosterone levels handicap the immune system (Kanda et al., 1996) and therefore only high quality males may be able to 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 might be preferred (Thornhill and Gangestad, 1999; Getty, 2002).

While masculine faced men are healthier (Rhodes et al., 2003; Thornhill and Gangestad, 2006), physically stronger (Fink et al., 2007), and more facially symmetric (Little et al., 2008b) than their feminine faced counterparts, masculinity in a partner also carries a cost. Masculine faced men are found to be more aggressive (Carre and McCormick, 2008) and more likely to pursue short-term relationships than feminine faced men (Boothroyd et al., 2008). Men with masculine faces also 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). As might be expected then, masculine faces are seen as more dominant but not seen as possessing traits that would be desirable in a long-term partner (Perrett et al., 1998; Boothroyd et al., 2007). 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, such as health or dominance, 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), some studies have reported that women with partners may be more likely to engage in extra-pair sexual activity at peak fertility (Baker and Bellis, 1995). Further evidence for possible extra-pair sexual behaviour 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 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 a different, but potentially complementary, explanation for shifting preferences, alterations in progesterone level have been associated with increased commitment to a partner, and increased preferences for less masculinised male faces during the luteal phase of the cycle (Jones et al., 2005). Similar findings for the link with progesterone are seen for preferences for masculine voices (Puts, 2006). This link with progesterone may reflect an increase in the care and support that is sought during times when a woman's hormonal profile is similar to that characterized in pregnancy (Jones et al., 2005). In this way, rather than acquiring indirect benefits for offspring from masculine men, women may instead maximize investment from feminine men when raised progesterone prepares the body for pregnancy (Jones et al., 2005).

Preferences for masculinity in faces have also been found to be moderated by other factors relating to potentially strategic choice. 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 so than females without a current romantic partner. Another factor that influences preferences for facial masculinity is the type of relationship being looked for. Studies have shown that women tend to prefer more masculine faces when judging for a short-term than for a long-term relationship (Little et al., 2002). Indeed, in a variety of studies, cycle effects are often more likely seen when women judge for short-term relations (reviewed in Gangestad and Thornhill, 2008; Jones et al., 2008). In a similar way to already having an investing partner, short-term relations minimise the need to value investment from partners. While studies have focused on male masculinity, symmetry is another putative cue to male health (Thornhill and Gangestad, 2006) and has also been found to vary across the cycle with studies showing both within- and between-subject shifts in preferences towards more symmetric faces at high fertility (Little et al., 2007c). Relationship status and relationship context appear to be important for cyclic shifts in preferences. Cyclic shifts in women's preferences for masculine characteristics in men's faces are generally greatest among women who already have romantic partners and when women judge men's attractiveness for short-term, extra-pair relationships (Penton-Voak et al., 1999; Little et al., 2007c; Gangestad and Thornhill, 2008; Jones et al., 2008). In particular, preferences appear to shift mainly for short-term contexts, when context has been examined, and indeed no study that has distinguished between short- and long-term contexts has shown a cycle shift for long-term judgements (reviewed in Gangestad and Thornhill, 2008; Jones et al., 2008). While there is indeed a growing body of evidence that shifts in preferences for masculine traits do occur across the cycle, some studies have not demonstrated these effects. There have been unsuccessful replications of cyclic variation in women's masculine face preferences. For example, two recent studies observed no evidence for cyclic variations in women's preferences for

masculine versus feminine male faces (Peters et al., 2009; Harris, 2011). Additionally, a recent study found that women preferred the faces of men with high testosterone levels at high fertility during the menstrual cycle, but observed no effect of cycle phase on women's preferences for male faces that were perceived to be masculine (Roney et al., 2011).

Although many studies have now demonstrated that women's preferences for the body odours of symmetric men are enhanced around ovulation (reviewed in Gangestad and Thornhill, 2008), evidence for cyclic shifts in women's preferences for symmetry in men's faces is equivocal. As noted, one paper presenting two studies, one between- and one within-subject, has found that women's preferences for symmetric male faces were stronger around ovulation than during other phases of the menstrual cycle, at least among partnered women or women who were instructed to judge men's attractiveness as short-term mates (Little et al., 2007c). By contrast, several other studies have observed no evidence for cyclic shifts in women's preferences for symmetric men's faces (Koehler et al., 2002; Cardenas and Harris, 2007; Oinonen and Mamanian, 2007; Peters et al., 2009), although one of the studies with a null finding for preference did find that women's ability to detect asymmetries in men's faces varied over the menstrual cycle in the predicted manner (Oinonen and Mamanian, 2007).

There are significant methodological differences between studies examining cycle effects making direct comparisons between those reporting null and positive effects difficult. Studies differ, for example, in stimuli number, stimuli type, and how fertility is defined. One key difference appears to be the issue of relationship context. Most studies reporting null results for preferences for masculine (Peters et al., 2009; Harris, 2011; Roney et al., 2011) and symmetric faces (Cardenas and Harris, 2007; Oinonen and Mamanian, 2007; Peters et al., 2009) have examined general attractiveness ratings and have not distinguished between short- and long-term contexts. Given larger cyclic shifts for short-term judgements and the general absence of effects for long-term judgements in some studies of facial masculinity and symmetry preferences, general attractiveness judgements may be less likely to show effects of cycle phase than judgements of men's attractiveness for short-term relationships, specifically.

The current study again examined preferences for masculinity and symmetry in male faces across the menstrual cycle, addressing the impact of short-term versus long-term context in a within-participant (Study 1) and between-participants study (Study 2). We predicted that women would prefer more masculine and symmetric male faces when in the follicular phase of their cycle. We also predicted that menstrual cycle shifts would be limited to short-term judgements and that there may be an interaction between fertility and relationship context if shifting preferences across the menstrual cycle serve to focus individuals on the quality of potential short-term partners.

2. Study 1

2.1. Participants

Twenty women (aged 17—27 years, mean age = 20.2 years, SD = 2.6 years) took part in the study. The study was conducted in the laboratory. Participants were volunteers who were paid £5 for participation and who were selected for reporting to be heterosexual, not using oral or other hormonal contraception, being between 17 and 40 years of age, and not being pregnant. The study was conducted in line with the Declaration of Helsinki and the British Psychological Association's ethical guidelines.

2.2. Cycle phase and conception risk

Initial email correspondence was used to ascertain basic cycle data and women were booked to come for their first session based on the closest available date which would place them either in the late follicular phase (days 6—14) or luteal phase (days 15—28 and we attempted to schedule women around day 24) of their cycle. 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 (women reporting days 8—14) and low (women reporting days 19—29) conception risk based on self-reports of the previous onset of menses. These groups correspond to the late follicular phase and the luteal phase respectively (e.g., Regan, 1996). On average, women in the late follicular phase were on day 10.9 (SD = 2.2) and those in the luteal phase were on day 22.2 (SD = 2.5) of their cycles. We additionally asked women to estimate how many days until their next menstruation. On average, women in the late follicular phase estimated 18.0 (SD = 5.9) days and those in the luteal phase estimated 6.3 (SD = 2.3, minimum of 2) days until next menstruation. All women answered "no" to the question: "Are your periods often irregular?"

To estimate fertility and 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 0.086. A paired samples *t*-test confirmed our follicular/high fertility group (mean = 0.063, SD = 0.021) was predicted to have a higher conception risk than our luteal/low fertility group (mean = 0.017, SD = 0.007, $t_{19} = 8.54$, $p < .001$). We note that our cycle phase split captures fertility but also offers insight into the hormonal profile of the responding women. In our split, those in the follicular phase should have higher oestrogen than progesterone while those in the luteal phase should have higher progesterone than oestrogen (Gilbert, 2000).

Test session was not randomised but there was no bias in whether women took part in the high or low fertile phase first (10 women came in first in the high fertile phase and 10 women came in first in the low fertile phase).

2.3. Stimuli

Masculinity: To measure preferences for sexually dimorphic features we used 10 pairs of composite male face images. Each pair comprised of one masculinised and one feminised version of the same face (see Fig. 1 for example images).

Figure 1 Examples of feminised (top left), masculinised (top right), asymmetric (bottom left), symmetric (bottom right) male faces.

Original images were 50 young adult Caucasian male and 50 female photographs taken under standard lighting conditions and with a neutral expression. The composite images were made by creating an average image made up of 5 randomly assigned individual facial photographs (this technique has been used to create composite images in previous studies, see e.g., Benson and Perrett, 1993; Tiddeman et al., 2001; Little and Hancock, 2002). Faces were transformed on a sexual dimorphism dimension using the linear difference in 2D shape between a composite of all 50 adult males and a composite of all 50 young adult females (following the technique reported in Perrett et al., 1998). Transforms represented ±50% the difference between these two composites (100% would represent the complete transform and so starting from a female face +100% towards male would make the face into a perceptually male shape). This meant that each face was transformed along the sexual dimorphism axis by the same amount, either increasing masculinity or increasing femininity, and that faces retained their identities and perceived sex (female faces remained female in appearance and male faces remained male in appearance). Composite images were made perfectly symmetric so that transforms did not alter symmetry.

Symmetry: To measure symmetry preferences, we used 15 stimulus pairs that have been used in previous studies (Perrett et al., 1999; Little et al., 2001; Little and Jones, 2003) which were 15 male Caucasian individuals between 20 and 30 years. Each pair was made up of one original and one symmetric image. All images were manipulated to match the position of the left and right eyes. To generate the symmetric images, original images were warped so that the position of the features on either side of the face was symmetrical. Images maintained original textural cues and were symmetric in shape alone. See Perrett et al. (1999) for technical details. An example of an original and symmetrical face can be seen in Fig. 1. The symmetry manipulation was independent of sexual dimorphism.

2.4. Procedure

Participants completed the tests twice, at two different points in their cycle. Cycle data was taken by the experimenter from the questionnaire at the first test session and a subsequent date for the second session was agreed at the end of the first test. A questionnaire was first administered addressing age, hormonal contraceptive use, days since last menstruation, pregnancy status, and sexuality followed by the face tests. Order of rating of short- and long-term contexts was randomly determined for each participant. Participants were presented with definitions of short- and long-term relationships 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).

The 10 pairs of masculine and feminine faces and the 15 pairs of symmetric and asymmetric faces were presented together. Faces were shown as pairs with both order and side of presentation randomised. Participants were asked to choose the face from the pair that they found most attractive. Clicking

on one of the buttons beneath the faces moved participants on to the next face trial.

2.5. Results

Percentage of masculine and symmetric faces chosen were calculated for each participant by taking the number of masculine or symmetric faces picked from the pairs (from 0 to 10 for masculinity and 0 to 15 for symmetry) and converting the score to a percentage.

For masculinity preferences, one-sample *t*-tests against no preference (i.e., the chance value of 50%) revealed that women preferred more masculine male faces for short-term relationships when fertile (short-term follicular, mean = 75.7%, SD = 15.5, $t_{19} = 7.41$, $p < .001$) and also, though not reaching significance, for long-term judgements when less fertile (long-term luteal, mean = 62.0%, SD = 28.0, $t_{19} = 1.92$, $p = .071$). Masculine faces were preferred but not significantly so for long-term relationships when fertile (long-term follicular, mean = 57. 5%, SD = 33.7, $t_{19} = 1.00$, $p = .332$) and for short-term judgements when less fertile (short-term luteal, mean = 57.7%, SD = 27.9, $t_{19} = 1.23$, $p = .232$). Collapsing across both term and cycle phase revealed significant overall preferences for masculinity (mean = 63.2%, SD = 18.7, $t_{19} = 3.17$, $p = .005$).

For masculinity preferences, a repeated measures ANOVA with term (short/long) and cycle phase (follicular/luteal) as within-participant factors revealed a significant interaction between cycle phase and term ($F_{1,19} = 4.99$, $p = .038$). There was no overall significant effect of cycle phase ($F_{1,19} = 2.77$, $p = .113$) or term ($F_{1,19} = 1.37$, $p = .256$). The interaction between cycle phase and term can be seen in Fig. 2 and indicates that women preferred more masculine faces in the follicular phase than in the luteal phase for short-term relationships more than for long-term relationships. Using separate paired sample *t*-tests for each term revealed a significant effect of cycle phase for judging faces for short-term relationships ($t_{19} = 3.21$, $p = .005$) but not for judging faces for long-term relationships ($t_{19} = 0.62$, $p = .541$).

For symmetry preferences, one-sample *t*-tests against no preference (50%, no preference) revealed that women preferred more symmetric male faces for short-term relationships when fertile (short-term follicular, mean = 64.0%, SD = 16.2, $t_{19} = 3.85$, $p < .001$) and long-term judgements when less fertile (long-term luteal, mean = 58.3%, SD = 17.3, $t_{19} = 2.16$, $p = .044$). Symmetric faces were preferred but not significantly so for long-term relationships when fertile (long-term follicular, mean = 56.7%, SD = 16.4, $t_{19} = 1.82$, $p = .085$) and for short-term judgements when less fertile (short-term luteal, mean = 55.7%, SD = 15.6, $t_{19} = 1.62$, $p = .122$). Collapsing across both term and cycle phase revealed significant overall preferences for symmetry (mean = 58.7%, SD = 11.4, $t_{19} = 3.39$, $p = .003$).

For symmetry preferences, a repeated measures ANOVA with term (short/long) and cycle phase (follicular/luteal) as within-participant factors revealed a significant interaction between cycle phase and term ($F_{1,19} = 5.90$, $p = .025$). There

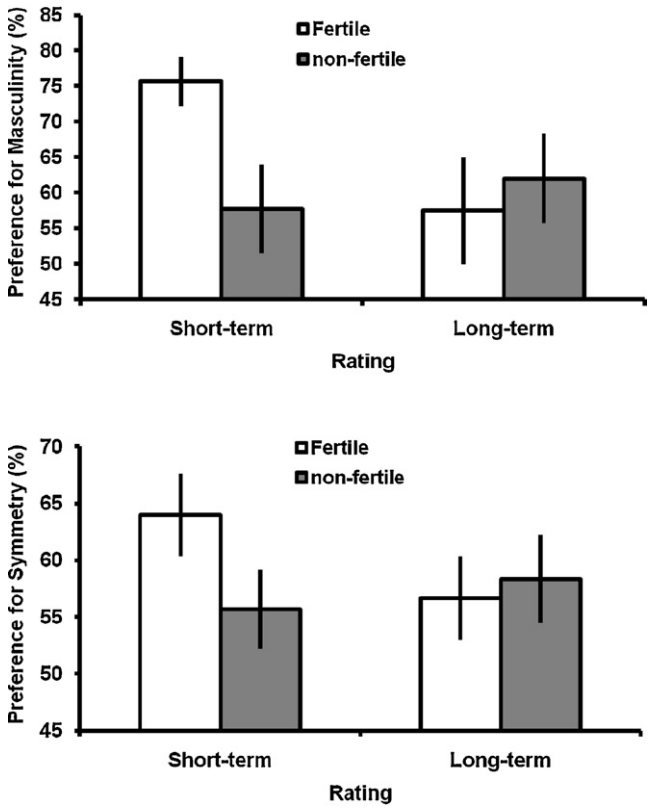

Figure 2 Study 1: % Preferences for facial masculinity (top) and symmetry (bottom) (±1SE of mean) by cycle phase noted as fertility (high/low) and rating by term (short/long). Note that the error bars show between-participant variance in preference, not within-participant variance. On the *y*-axis, 50% is chance.

was no overall significant effect of cycle phase ($F_{1,19} = 1.35$, $p = .260$) or term ($F_{1,19} = 0.04$, $p = .557$). The interaction between cycle phase and term can be seen in Fig. 2 and indicates that women preferred more symmetric faces in the follicular phase than in the luteal phase for short-term relationships more than for long-term relationships. Using separate paired sample *t*-tests for each term revealed a significant effect of cycle phase for judging faces for short-term relationships ($t_{19} = 3.32$, $p = .004$) but not for judging faces for long-term relationships ($t_{19} = 0.39$, $p = .704$).

3. Study 2

3.1. Participants

Two hundred and thirty four women (aged 17—40 years, mean age = 26.8 years, SD = 6.2 years) took part in the study. The study was conducted in over the Internet. Participants were volunteers who took part when visiting a research website and who were selected for reporting to be heterosexual, not using oral or other hormonal contraception, being between 17 and 40 years of age, having a cycle length less than 29 days, and not being pregnant. The study was conducted in line with the Declaration of Helsinki and the British Psychological Association's ethical guidelines.

3.2. Cycle phase and conception risk

Cycle phase was determined in the same way as in Study 1 although no booking was made and so participants could be on any day in their cycle. We then classified those in the follicular phase as reporting days 6—14 of their cycle (79 women) and classified all other women as non-follicular (155 women). On average, women in the follicular phase were on day 10.3 (SD = 2.9). All women answered "no" to the question: "Are your periods often irregular?"

We also estimated fertility as in Study 1. A paired samples *t*-test confirmed our follicular/high fertility group (mean = 0.054, SD = 0.029) was predicted to have a higher conception risk than our non-follicular/low fertility group (mean = 0.023, SD = 0.022, $t_{232} = 9.20$, $p < .001$).

3.3. Stimuli

Stimuli were made in an identical way to Study 1 except that only 5 pairs of masculine/feminine images and 5 pairs of symmetric/asymmetric images were used.

3.4. Procedure

The procedure was identical to Study 1 except that participants only took the tests once and saw only 5 pairs of masculine/feminine images and 5 pairs of symmetric/asymmetric images.

3.5. Results

Percentage of masculine and symmetric faces chosen were calculated for each participant by taking the number of masculine or symmetric faces picked from the pairs (from 0 to 5 for masculinity and 0 to 5 for symmetry) and converting the score to a percentage.

For masculinity preferences, one-sample *t*-tests against no preference (i.e., the chance value of 50%) revealed that women preferred more masculine male faces for short-term relationships when fertile (short-term follicular, mean = 58.9%, SD = 15.7, $t_{78} = 5.05$, $p < .001$), for long-term judgements when less fertile (long-term non-follicular, mean = 55.0%, SD = 15.8, $t_{154} = 3.95$, $p < .001$) and for short-term judgements when less fertile (short-term non-follicular, mean = 54.5%, SD = 14.5, $t_{154} = 3.90$, $p < .001$). Masculine faces were preferred but not significantly so for long-term relationships when fertile (long-term follicular, mean = 53.2%, SD = 16.1, $t_{78} = 1.78$, $p = .078$).

For masculinity preferences, a repeated measures ANOVA with term (short/long) and cycle phase (follicular/non-follicular) as within-participant factors revealed a significant interaction between cycle phase and term ($F_{1,232} = 5.07$, $p = .025$). There was no overall significant effect of cycle phase ($F_{1,232} = 0.63$, $p = .427$) or term ($F_{1,232} = 3.68$, $p = .056$), although the latter was close to being significant. The interaction between cycle phase and term can be seen in Fig. 3 and indicates that women preferred more masculine faces in the follicular phase than in the non-follicular phase for short-term relationships more than for long-term relationships. Using separate paired sample *t*-tests for each term revealed a significant effect of cycle phase for judging faces for short-term relationships ($t_{232} = 2.12$, $p = .035$) but not for judging faces for long-term relationships ($t_{232} = 0.71$, $p = .421$).

For symmetry preferences, one-sample *t*-tests against no preference (50%, no preference) revealed that women preferred more symmetric male faces for short-term relationships when fertile (short-term follicular, mean = 66.6%, SD = 24.3, $t_{78} = 6.06$, $p < .001$), for long-term relationships when fertile (long-term follicular, mean = 58.5%, SD = 22.8, $t_{78} = 3.30$, $p = .001$), for long-term judgements when less fertile (long-term non-follicular, mean = 59.4%, SD = 21.1, $t_{154} = 5.53$, $p < .001$), and for short-term judgements when less fertile (short-term non-follicular, mean = 57.7%, SD = 24.0, $t_{154} = 3.98$, $p < .001$).

For symmetry preferences, a repeated measures ANOVA with term (short/long) as a within-participant factor and cycle phase (follicular/non-follicular) as a between-participant factor revealed a significant interaction between cycle phase and term ($F_{1,232} = 5.51$, $p = .020$). There was no overall significant effect of cycle phase ($F_{1,\ 232} = 2.83$, $p = .094$) or term ($F_{1,\ 232} = 2.38$, $p = .125$). The interaction between cycle phase and term can be seen in Fig. 3 and indicates that women preferred more symmetric faces in the follicular phase than in the non-follicular phase for short-term relationships more than for long-term relationships. Using separate independent samples *t*-tests for each term revealed a significant effect of cycle phase for judging faces for short-term relationships ($t_{232} = 2.67$, $p = .008$) but not for judging faces for long-term relationships ($t_{232} = 0.29$, $p = .771$).

4. Discussion

Study 1 (within-participants) and Study 2 (between-participants) demonstrated that women's preferences for manipulated masculinity and symmetry in men's faces change during

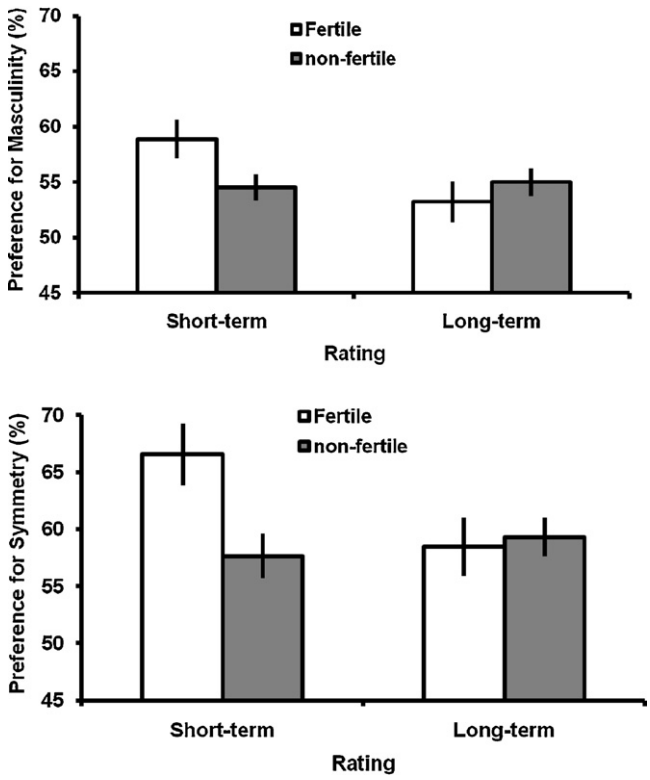

Figure 3 Study 2: % Preferences for facial masculinity (top) and symmetry (bottom) (±1SE of mean) by cycle phase noted as fertility (high/low) and rating by term (short/long). On the *y*-axis, 50% is chance.

the menstrual cycle and that women show the greatest change during the cycle when judging men's attractiveness for short-term relationships. Across context and cycle phase the preferences for symmetry in faces are in line with previous results (Perrett et al., 1999; Little et al., 2008b), and, while studies have produced mixed results for preferences for masculinity, the masculinity preferences seen here are in line with previous studies using these images (Little et al., 2008b).

Women preferred masculine and symmetric faces at peak fertility here only for short-term relationships, and this suggests that these traits may be more highly valued under circumstances where the potential to pass traits to offspring is high and where parental investment is not considered as important. 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. Indeed, women are more likely to fantasise about another man if their current partner is less sexually attractive (Haselton and Gangestad, 2006) or more asymmetric (Gangestad et al., 2005). Functionally, shifting preferences may then lead to maximizing the likelihood that offspring inherit strong immune systems or high dominance via good genes from fathers (Penton-Voak and Perrett, 2000) or promote strategies to associate with more investing individuals when raised progesterone prepares the body for pregnancy (Jones et al., 2005). Consistent with the latter view, preferences for self-resemblance in faces are increased when progesterone is high in the cycle (DeBruine et al., 2005). Such logic of differences in investment is applicable to both masculinity and symmetry given both are proposed to be markers of indirect benefits (Little et al., 2011) and high quality may lead to low investment strategies in men (Gangestad and Simpson, 2000).

Three studies have observed no evidence for cyclic variations in women's preferences for masculine versus feminine male faces (Peters et al., 2009; Harris, 2011; Roney et al., 2011) and two studies have observed no evidence for cyclic shifts in women's preferences for symmetric men's faces (Oinonen and Mamanian, 2007; Peters et al., 2009). In all of these studies, the authors addressed general attractiveness judgements and did not distinguish between short- and long-tem contexts. The current study suggests that these null effects occurred because of larger cyclic shifts for short-term judgements and a general absence of effects for long-term judgements (Little et al., 2007c; Gangestad and Thornhill, 2008). General attractiveness judgements may be less likely to show the relevant effects. We do note that some studies have also not distinguished between relationship contexts and shown positive results. For example, one study using unmanipulated faces found that preferences for masculine male faces was higher at high fertility, though perhaps critically, this effect was seen only in women who already had a partner (Little et al., 2008a). This is suggestive that studies should address at least relationship context or relationship status in order to increase confidence that effects will be observed and that we should be cautious of accepting null results for studies that ignore these important variables.

Another possible explanation of the null findings comes from studies that suggest the extent to which women's

preferences change over the menstrual cycle vary systematically among women. For example, cyclic variation in women's preferences for masculine characteristics in men's voices is significantly greater among women with high trait (i.e., average) oestrogen levels than it is among women with relatively low trait oestrogen levels (Feinberg et al., 2006). This pattern of results may occur because varying their sexual strategy during the menstrual cycle may benefit unattractive women more than it benefits attractive women (Feinberg et al., 2006). Given differences between women in fantasising about another man vary according to partner attractiveness (Gangestad et al., 2005; Haselton and Gangestad, 2006), partner attractiveness and relationship satisfaction are also likely important variables in addressing cycle shifts in preferences. Women who have partners they consider sexually attractive and women who are satisfied in their relationship may be less likely to show cycle shifts.

There are of course other methodological differences between studies. Research on facial attractiveness has used both real and computer graphic manipulated faces but studies on cyclic shifts have generally used manipulated faces. Computer graphic studies which manipulate masculinity have tended to suggest that feminine male faces are attractive while studies of real faces using rated masculinity have usually demonstrated preferences for masculinity (see Rhodes, 2006). This has led Rhodes (2006) to suggest that real faces may reveal a truer picture of women's preferences than computer manipulated images. Following this claim, in one study presenting a null results for cycle shift for both perceived masculinity and symmetry in unmanipulated images, researchers have suggested that cyclic shifts in women's masculinity preferences may be an artefact of the computer graphic methods (Peters et al., 2009). Such a claim is, however, difficult to reconcile with earlier findings from a study that demonstrated cyclic shifts in women's preferences for masculinity in real (i.e., unmanipulated) face images (Little et al., 2008a). This claim is also problematic given the converging evidence for cyclic shifts in women's preferences for masculinity from studies that have assessed preferences for masculinity in other domains (e.g., behaviour, personality descriptions, body odour). Finally, it is also important to note that cycle effects are seen in studies that did not use computer graphics to prepare their stimuli (e.g., Gangestad et al., 2004, 2007). Overall, differences between stimuli types used for measuring face preferences appear unlikely to generate large differences in the general direction of cycle studies.

Lastly, two null findings using identical methodology did address relationship context, though not relationship status (Koehler et al., 2002, 2006). One issue with these studies is that high and low fertility were calculated differently here than in other studies as the authors compared early and late follicular phases. Since conception risk is higher in the late follicular phase than luteal phase, and the late follicular phase and highest progesterone test session from the luteal phase should also differ markedly in progesterone level, this comparison captures differences in both fertility and progesterone level (Gilbert, 2000). By contrast, comparing the early and late follicular phases (Koehler et al., 2002, 2006) will capture differences in fertility but not progesterone level. Given researchers have argued progesterone may be an important component of cyclic preferences shifts (Jones et al., 2005; Puts, 2005), a null result when examining women across the cycle this way may be unsurprising. There are other potentially significant methodological differences between studies examining cycle effects making direct comparisons between those reporting null and positive effects difficult. The influence of stimuli number, stimuli type, and how fertility is defined remain to be fully addressed in studies of shifting preferences across the menstrual cycle. There are additional sources of variation across studies, for example small sample sizes may also lead to overall null effects in some cycle studies and given masculinity and symmetry preferences vary across cultures (Little et al., 2007a; DeBruine et al., 2010) differences in effects might also be the result of differences between populations.

In summary, the current studies suggest that the menstrual cycle has an impact on face preferences, with women preferring more masculine and more symmetric faces at peak fertility. We suggest that ideas of evolved mechanisms promoting attention to biologically relevant traits at peak fertility may provide a parsimonious explanation for the observed results. Hormonal changes associated with phases of the menstrual cycle likely provide the mechanism for these differences in preference. While some studies have demonstrated null results for cycle shifts for the same traits, variation appears linked to factors such as relationship context here and relationship status in other studies and therefore null results in studies that do not account for these factors may be inconclusive. Future studies can address the relative potential for various factors to moderate cycle effects as such effects are clearly complex.

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Conflict of interest statement

None.

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