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Preferences for symmetry in faces change across the menstrual cycle

Anthony C. Little [a,b,*], Benedict C. Jones [c], D. Michael Burt [d], David I. Perrett [e]

[a] *School of Psychology, University of Stirling, UK*
[b] *School of Biological Sciences, University of Liverpool, UK*
[c] *School of Psychology, University of Aberdeen, UK*
[d] *School of Psychology, University of Durham, UK*
[e] *School of Psychology, University of St. Andrews, UK*

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Abstract

Symmetry in human male faces may be a cue to heritable fitness benefits and is found attractive. Preferences for facial masculinity, another proposed marker of genetic quality, have been found to vary in ways that may maximise evolutionary relevant benefits and masculinity is found to be of increased attractiveness at peak fertility across the menstrual cycle. Here we show that women prefer more symmetric faces at peak fertility (Study 1) and that such shifting preferences may be potentially strategic preferences as we found them to occur only for judgements concerning short-term relations and when women already had a partner (Study 2). Such preferences potentially indicate a strategy that maximises the quality of extra-pair/short-term partners or a quality dependent response to hormones. Such strategic preferences for symmetry may support the role of symmetry in signalling potential good-gene benefits.

Keywords: Symmetry; Facial attractiveness; Menstrual cycle; Preferences; Hormones; Mate choice

Symmetry is found attractive by many animals (see review by Møller and Thornhill, 1998). Studies of naturally occurring human facial asymmetries show that measured symmetry is positively correlated with attractiveness judgments (Grammer and Thornhill, 1994; Jones et al., 2001; Mealey et al., 1999; Penton-Voak et al., 2001; Rhodes, 2006; Scheib et al., 1999). Consistent with preferences for naturally occurring symmetry in real faces, computer graphic studies (Little et al., 2001; Perrett et al., 1999; Rhodes, 2006; Rhodes et al., 1998) have shown preferences for faces manipulated to increase symmetry, including cross-cultural (Rhodes et al., 2001) and cross-species (Waitt and Little, 2006) agreement on the attractiveness of symmetry.

Preference for symmetric faces has been explained as an evolutionary adaptation to identify high-quality mates (Thornhill and Gangestad, 1999), though we note the issue is controversial and that some authors have argued that symmetry preferences may arise without recourse to adaptation (e.g., Johnstone, 1994). Symmetry in human faces has been linked to potential heritable fitness ('good-genes') because symmetry is a useful measure of the ability of an organism to cope with developmental stress (both genetic and environmental). Fluctuating asymmetry, asymmetry that has a normal distribution around a mean of zero (Valen, 1962), is thought to be particularly important. As the optimal developmental outcome of most characters is symmetry, deviation from perfect symmetry can be considered a reflection of challenges to development. Only high quality individuals can maintain symmetric development under environmental and genetic stress and therefore symmetry can serve as an indicator of phenotypic quality as well as genotypic quality (e.g., the ability to resist disease, Møller, 1997; Møller and Thornhill, 1998, for reviews). In line with these ideas, morphological symmetry appears to be related to reproductive success in many species, including humans (Gangestad and Thornhill, 1997; Møller and Thornhill, 1998). For example, more symmetric human males report more sexual partners than less symmetric men (Thornhill and Gangestad, 1994).

Sexual dimorphism in human faces is another proposed marker of genetic quality (Thornhill and Gangestad, 1999) and has been much studied in terms of strategic preferences. The relationship between attractiveness and male facial masculinity

* Corresponding author at: School of Psychology, University of Stirling, Stirling, FK9 4LA Scotland, UK. Tel.: +44 1786 467651; fax: +44 1786 467641.
E-mail address: anthony.little@stir.ac.uk (A.C. Little).

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is not clear cut though, some findings showing attraction to masculinity (Cunningham et al., 1990; DeBruine et al., 2006; Grammer and Thornhill, 1994) and others showing attraction to femininity (Berry and McArthur, 1985; Cunningham et al., 1990; Little and Hancock, 2002; Perrett et al., 1998; Rhodes et al., 2000). Human males bring two factors to a parenting relationship: a level of paternal investment and potential heritable benefits (e.g., genes for high quality immune systems). The perceived high dominance and lower levels of co-operation point to lower paternal investment from the owners of masculine faces (Perrett et al., 1998). In the context of a short-term relationship the perceived cues to high paternal investment in the feminine faced male are of little value to a female. Females may therefore seek to maximise the genetic fitness of potential offspring if they are not extracting any other benefits from their mates. In long-term relationships, better parenting and increased co-operation may outweigh the benefits of genetic fitness, thereby enhancing the attractiveness of feminine-faced males. Indeed, studies have shown that masculinity in male faces and physical attractiveness are preferred more in short-term than in long-term contexts (Little et al., 2002; Scheib, 2001).

An increased preference for genetic fitness over signs of parental investment would also be expected in extra-pair copulations when a woman has already acquired a long-term partner. Little et al. (2002) have also shown that women who have partners prefer masculinity in faces more than those without a partner. Linking to symmetry, women have been found to prefer pictures of men with symmetrical bodies as extra-pair partners (Gangestad and Thornhill, 1997).

Shifting female preferences for masculine facial traits are also seen across the menstrual cycle. During the follicular phase of the menstrual cycle when conception is most likely, women prefer relatively masculine male faces (Frost, 1994; Johnston et al., 2001; Jones et al., 2005a,b; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999). Women fantasise more about extra-pair relations at peak fertility (Gangestad et al., 2002) and report being less committed to their partners during the late follicular (i.e. fertile) phase of the cycle than at other times (Jones et al., 2005a,b). These data are suggestive of a possible mechanism where women may maximise their chances of becoming pregnant with the offspring of males chosen for extra-pair affairs (Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999). Interactions are also evident with other variables outlined above with there being trends for women who have partners and rating for short-term relationships showing the largest cyclic shifts (Penton-Voak et al., 1999), and that fertile women relatively prefer videos of dominant behaviour (Gangestad et al., 2004) and masculine bodies (Little et al., 2007) only when judging for short-term relationships. Such males may be selected for possessing superior or alternative genes to the woman's current partner. Of course a mechanism to attend to quality in males when most likely to become pregnant may also serve to maximise genetic benefits in offspring for women without partners. Studies do show that women prefer the odour of more symmetrical males at peak fertility (Rikowski and Grammer, 1999; Thornhill et al., 2003) but one previous study has shown no influence of the menstrual cycle on preferences for facial symmetry indicating that menstrual cycle shifts do not take place for symmetry (Koehler et al., 2002). This result has been subsequently replicated using the same methodology by the same group (Koehler et al., 2006). Another study has shown that symmetry detection is better at peak fertility but this advantage did not carry over to preferences (Oinorten and Mamanian, 2007), which does suggest the cycle plays a role in symmetry perception.

Symmetry in male partners, like masculinity, potentially carries a cost to choosing females. It has been argued that high-quality males are less likely to invest in mates and instead pursue a strategy of maximising their number of lifetime mates (Gangestad and Simpson, 2000). Indeed, men with high body symmetry appear less inclined to provide paternal care than other men (Gangestad and Simpson, 2000) and symmetric men appear more inclined to engage in physical conflict with other men (Furlow et al., 1998). Thus we may expect similarities in potentially strategic preferences for symmetry and masculinity as symmetry is also associated with potential genetic benefits and decreased levels of parental investment in humans.

1. Study 1

Following studies showing preferences for facial masculinity are higher at peak fertility (Frost, 1994; Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999), in Study 1 we tested for change in preference for facial symmetry across the menstrual cycle using a powerful within-participant design. Koehler et al. (2002) previously found no difference in attraction to symmetry in faces when preferences during the early and late follicular phases of the menstrual cycle were compared. Although the early and late follicular phases of the menstrual cycle differ in fertility they do not differ in progesterone level (Gilbert, 2000). Changes in face preferences during the menstrual cycle have been linked to change in progesterone level across the cycle in two different studies, however (DeBruine et al., 2005; Jones et al., 2005a,b), and changes in progesterone appear involved in menstrual cycle shifts in preferences for masculinity in both faces (Jones et al., 2005a,b) and voices also (Puts, 2005). Jones et al. (2005a) also found that predicted progesterone level during the menstrual cycle was associated with women's commitment to their romantic partner. We therefore compared attraction to symmetry in male and female faces in the late follicular phase of the menstrual cycle and on the days between ovulation and onset of menses with the highest urinary concentration of progesterone metabolites. 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) will capture differences in fertility but not progesterone level.

Following previous findings implicating change in progesterone level for cyclic variation in preferences for putative cues to men's genetic fitness (facial and vocal masculinity, Jones et al., 2005a; Puts, 2005), we predicted that women would demonstrate stronger preferences for symmetry when at the more fertile phase of the menstrual cycle than when progesterone is high during the luteal phase of the cycle. We also presented male and female faces to test whether sex of face interacted with preference across cycle phase. As oral contraception use has been found to influence women's preferences for potentially adaptive genetic benefits (e.g., Little et al., 2002; Penton-Voak et al., 1999) we examined only those who reported no hormonal contraception use.

2. Methods

2.1. Participants

Thirty-one heterosexual women (aged 18–23, mean = 19.5, S.D. = 1.29) reporting regular menstrual cycles and non-use of oral contraceptives were tested at approximately weekly intervals on up to six occasions.

2.2. Stimuli

Pairs of male and female faces that varied only in symmetry of 2D shape and were identical in all other regards were manufactured. The method used to manufacture these images was identical to that used by Perrett et al. (1999) in their Study 2. Briefly, a composite male face was manufactured by averaging the shape, colour and texture from six individual male faces (mean age = 20.4 years). This composite face was then warped into the shape of each of the six individual faces and also into the shape of symmetric versions of each of the six individual faces. Symmetric shapes were defined by averaging an original face shape and a mirror-reflected version of itself. This process created six pairs of male faces, each pair consisting of two versions of the same face that differed only in symmetry of 2D shape. In the same way, six pairs of asymmetric and symmetric female faces (mean age = 19.8 years) were also manufactured. An example of an original and symmetrical face can be seen in Fig. 1.

2.3. Procedure

In each test session, participants completed a face preference test in which the symmetric and asymmetric versions of each of the 12 faces were presented side-by-side onscreen in a two-alternative forced choice paradigm and the participant instructed to chose the more attractive face. Symmetry stimuli were interspersed with filler trials (i.e. 24 pairs of face images that did not differ in symmetry but did differ in other dimensions, e.g., apparent age). Trial order was randomised, as was allocation of symmetric and asymmetric images to the left and right sides of the screen. Participants reported their typical cycle lengths and the number of days since their last period of menstrual bleeding. Participants were also instructed to provide a urine sample taken midstream from the first urination of each test day.

2.4. Processing of data

For each woman, the expected day of ovulation was identified from the reported date of onset for two periods of menstrual bleeding (backward counting 14 days from the second period). Test days that occurred between 0 and 7 days prior to the suspected date of ovulation were assigned to the late follicular (i.e. fertile) phase of the menstrual cycle. The test day on which concentration of progesterone metabolites (as indicated by pregnanediol:creatinine ratios) was highest in the urine sample was assigned to the high progesterone (i.e. 'mid-luteal') phase. Following Jones et al. (2005a,b), participants for whom the highest recorded concentration of progesterone metabolites in their urine was <0.5 were excluded from analyses because their hormonal profile suggested ovulation had not occurred during the cycle (Bonello and Norman, 2002). Following this process, there were valid high progesterone (mean = 6.14 days until onset of next period, range = 1–11 days until onset of next period) and late follicular (mean = 16.86 days until onset of next period, range = 14–20 days until onset of next period) phase test days for 19 participants. Concentration of progesterone metabolites in urine was higher on high progesterone test days (mean pregnanediol:creatinine ratio = 1.06, S.D. = 0.44) than on late follicular test days (mean pregnanediol:creatinine ratio = 0.32, S.D. = 0.11) for all participants ($t_{18} = 7.32$, $p < 0.001$). Assigning test days to the late follicular and high progesterone phases did not cause an order of testing effect ($p = 0.75$). The mean proportion of trials of which the symmetric male face was chosen was calculated separately for test days assigned to the high progesterone and late follicular phases. Corresponding values were also calculated for judgements of female faces.

3. Results

All tests are presented two-tailed. D denotes Cohen's D and η_p^2 denotes partial Eta^2.

Fig. 1. Asymmetric original (left) and symmetrical (right) male faces used in Study 2.

A one-sample *t*-test against chance revealed a significant preference for symmetry in faces in the late follicular phase (mean = 63%, S.D. = 12.0, $t_{18} = 4.74$, $p < 0.001$, $D = 2.234$), but not in the high progesterone phase (mean = 55%, S.D. = 13.1, $t_{18} = 1.75$, $p = 0.097$, $D = 0.825$). A repeated measures ANOVA was conducted with 'face-sex' (male/female) and 'cycle phase' (late follicular/high progesterone) as within-participant factors. This analysis revealed a main effect of cycle phase ($F_{1,18} = 5.72$, $p = 0.028$, $\eta_p^2 = 0.241$) and no other significant effects (all $F < 1.00$, all $p > 0.33$, all $\eta_p^2 < 0.060$). Preferences for symmetric faces were stronger in the late follicular phase than on days of the menstrual cycle with raised progesterone. We note that there was no interaction between face sex and phase ($F_{1,18} = 0.21$, $p = 0.65$, $\eta_p^2 = 0.012$), male faces: late follicular (*M* = 64%, S.D. = 12.2), highest progesterone (*M* = 58%, S.D. = 16.1), female faces: late follicular (*M* = 62%, S.D. = 17.3), highest progesterone (*M* = 53%, S.D. = 21.0).

4. Discussion

The results of Study 1 are strong evidence that preference for facial symmetry changes across the menstrual cycle. Symmetric faces are preferred more when women are more fertile. Although Koehler et al. (2002) show no effect of menstrual cycle on symmetry preference, it is worth noting that Koehler et al. (2002) used a different classification of high and low conception risk (comparing early and late follicular phases), that will not have tapped possible effects of change in progesterone level (since the early and late follicular phases are both characterised by low progesterone level). Tapping change in progesterone level may be important however since previous studies of cyclic shifts in preferences for masculine faces and voices and in women's reported commitment to their romantic partners have emphasised the importance of change in progesterone level for cyclic shifts in women's preferences and attitudes (Puts, 2005; Jones et al., 2005a). See also Jones et al. (2005a,b) and DeBruine et al. (2005) for further evidence that change in progesterone level may play an important role in cyclic shifts in women's face preferences.

We note that menstrual cycle shifts were seen for female faces in Study 1. While it is tempting to infer from this that cyclic variation in symmetry preference are unlikely to reflect adaptations for increasing offspring health, preferences for symmetry in stimuli other than faces, or indeed the female faces in Study 1, may be low-cost by-products of adaptive preferences for cues of genetic fitness in potential mates. Indeed, Jones et al. (2005a) observed cyclic shifts in women's preferences for masculinity in both male and female faces and noted that cyclic shifts in preferences for masculine women may be a low-cost by-product of adaptive variation in the strength of attraction to facial cues that signal genetic fitness in men.

5. Study 2

Preferences for facial masculinity have been found to vary in ways that may maximise evolutionary relevant benefits in women in a potentially strategic way. Increased preferences for masculinity are seen when women are judging at peak fertility in the menstrual cycle (as noted above), when judging for short- compared to long-term relationships (Little et al., 2002) and when women already posses a partner (Little et al., 2002). Studies suggest that cycle effects are greater when women have a partner (Penton-Voak et al., 1999) or when rating for short-term relationships (Gangestad et al., 2004; Little et al., 2007; Penton-Voak et al., 1999). Study 2 looked to examine how these two variables influence women's preferences for symmetry in male faces in interaction with cycle effects. Again here we examined only those who reported no hormonal contraception use.

Following Study 1 we predicted that women would have stronger preferences for symmetry when at the more fertile phase of the menstrual cycle than at other times. Following findings for preferences for masculinity in faces, bodies, and behavioural displays we also predicted potential interactions such that (1) women would have stronger preferences for symmetry at peak fertility when rating for short-term than for long-term relationships and (2) women would have stronger preferences for symmetry at peak fertility if they had a partner than if they did not have a partner. There was also the possibility of a three-way interaction amongst fertility, partnership and term.

6. Methods

6.1. Participants

Participants were recruited to participate both in the laboratory and over the Internet. Two hundred and ten volunteer heterosexual female participants who reported no hormonal contraceptive use (49 lab, 161 Internet, aged 18–35 mean = 25.0, S.D. = 4.8) took part in the study. Of the women 98 were in a relationship and 112 were not and 63 were classified as being in the follicular phase and 147 were not (see below).

6.2. Stimuli

Original images were 15 male Caucasian individuals between 20 and 30 years. From these pairs of images were created. Each pair was made up of one original and one symmetric image. These pairs have been used in previous studies (Little et al., 2001; Little and Jones, 2003; Perrett et al., 1999). All images were manipulated to match the position of the left and right eyes. Symmetric images were warped so that the position of the features on either side of the face was symmetrical. An example of an original and symmetrical face can be seen in Fig. 2.

6.3. Procedure

Participants were presented with two images of the same individual, an original and a symmetrically remapped version. The images were presented side by side on screen with the instructions: "Which face is the most attractive?" and "Please click the face which you feel is most attractive". Clicking on a box below the faces moved onto the next of the 15 image pairs. Participants judged all of the faces twice in two blocks, once with instructions to rate for a long-term relationship and once with instructions to rate for a short-term relationship. The rating (short- and long-term), image order and side of presentation were randomised. Participants also completed a questionnaire, administered on computer screen which addressed, age, sexuality, partnership status (Do you currently have a partner? Yes/No), hormonal-contraceptive use and days since last menstruation.

Fig. 2. Asymmetric original (left) and symmetrical (right) male faces used in Study 1.

6.4. Calculating conception risk

Following previous studies of preferences (Gangestad and Thornhill, 1998; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), we used a standard 28-day model of the female menstrual 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). Similar divisions have also been used in measuring risk-taking behaviour across the menstrual cycle (Chavanne and Gallup, 1998).

The mean days since menstruation for the fertile grouping was 10.4 (S.D. = 2.7). For the less fertile grouping, 37 women reported days 0–5 (mean = 2.9, S.D. = 1.8) and 110 women reported days 15–40 (mean = 20.7, S.D. = 4.3). To check whether our split captured differences in fertility we calculated predicted 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. (2001) 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 confirmed that our high fertility group (mean = 0.057, S.D. = 0.022) was predicted to have a higher conception risk than our low fertility group (mean = 0.023, S.D. = 0.027, $t_{208} = 9.46$, $p < 0.001$).

7. Results

A one-sample *t*-test against chance revealed a significant preference for symmetrical male faces in both the long-term (mean = 52%, S.D. = 1.4, $t_{209} = 2.47$, $p = 0.014$, $D = 0.342$) and short-term conditions (mean = 55%, S.D. = 1.5, $t_{209} = 4.97$, $p < 0.001$, $D = 0.688$). A paired sample *t*-test between short- and long-term preferences revealed a significantly greater preference for symmetry for short-term relationships ($t_{209} = 2.17$, $p = 0.031$, $D = 0.300$).

A repeated measures ANOVA was carried out with 'Term' (long/short) as a within-subject factor and 'Partner' (yes/no), 'Fertility' (high/low) and 'Test' (lab/Internet) as between-subject factors. Age was entered as a covariate. A preliminary analysis including the factor 'Order of term judgement' (short-term first/long-term first) revealed no significant effects involving this factor (all $F_{1,201} < 2.43$, $p > 0.12$, $\eta_p^2 < 0.012$).

The ANOVA revealed a significant interaction between 'Term' and 'Fertility' ($F_{1,201} = 6.54$, $p = 0.011$, $\eta_p^2 < 0.031$). Using an independent samples *t*-test we found that women preferred more symmetric faces for short-term relationships when they were in the fertile versus less-fertile phase ($t_{208} = 3.91$, $p < 0.001$, $D = 0.542$) but for long-term relationships phase did not significantly impact on preference ($t_{208} = 0.33$, $p = 0.74$, $D = 0.046$). From Fig. 3A it can been seen that this reflected women in the follicular phase preferred symmetry more for short-term than for long-term relationships.

There was no overall effect of term ($F_{1,201} = 2.40$, $p = 0.12$, $\eta_p^2 < 0.012$) when assessed alongside other factors and no other factors interacted with term (all $F_{1,201} < 1.02$, $p > 0.31$, $\eta_p^2 < 0.005$).

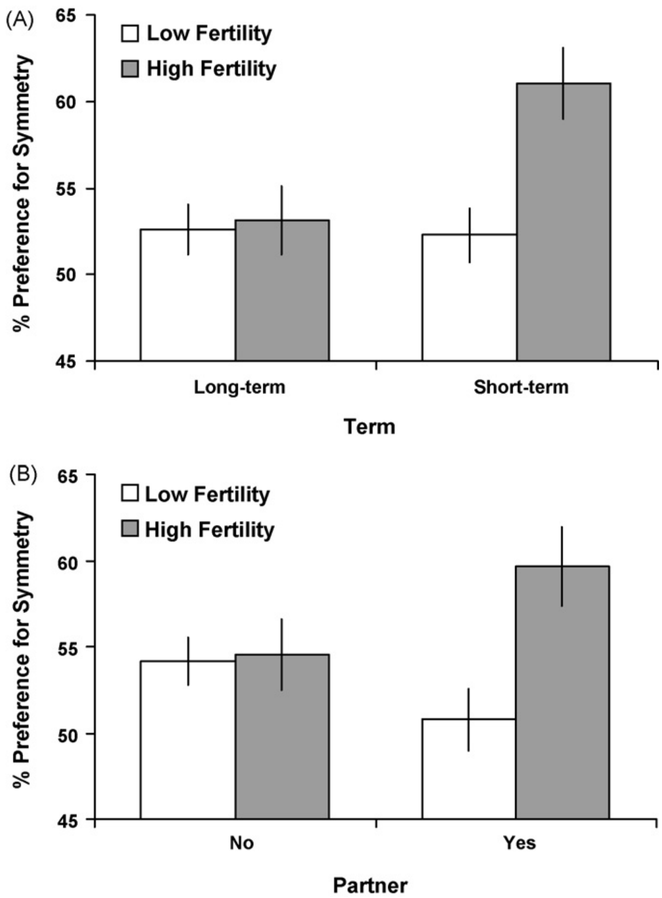

Fig. 3. Symmetry preferences (±1S.E. of mean) according to (A) term (short- and long-term) and fertility (high and low) and (B) partnership status (no partner and partner) and fertility (high and low).

For the between-participant effects there was a significant effect of age ($F_{1,201} = 6.34$, $p = 0.013$, $\eta_p^2 < 0.031$) and 'Fertility' ($F_{1,201} = 6.14$, $p = 0.014$, $\eta_p^2 < 0.030$), and a significant interaction between 'Partner' and 'Fertility' ($F_{1,201} = 5.02$, $p = 0.026$, $\eta_p^2 < 0.024$).

Following the significant effect of age as a covariate, positive correlations were found between age and symmetry preferences though the correlation was significant only for long-term judgements ($r = 0.18$, $p = 0.011$) and not short-term judgements ($r = 0.11$, $p = 0.13$). Using a Fisher's r-to-z transform revealed that there was no significant difference between these co-efficients ($z = 0.73$, $p = 0.465$). The main effect of Fertility was qualified by higher order interactions. For the interaction between Partner and Fertility, taking the average symmetry preference for short- and long-term judgements and using an independent samples t-test, we found that when women did not have a partner they did not significantly differ in their preference for symmetry between high and low fertility ($t_{111} = 1.05$, $p = 0.298$, $D = 0.200$) but when women had a partner preferences of high and low fertility women did differ ($t_{97} = 1.68$, $p = 0.096$, $D = 0.341$), though this was not conventionally significant. Fig. 3B shows that women in the follicular phase with partners show the greatest preference for symmetric faces.

No other factors or interactions were significant (all $F_{1,201} < 2.00$, $p > 0.16$, $\eta_p^2 < 0.010$).

8. Discussion

The results of Study 2 show that women have different face preferences for short- and long-term mates according to their fertility. In Study 2 only when women judged faces for short-term relationships did they show shifts in symmetry preferences across the menstrual cycle, suggesting that symmetry is important when most likely to become pregnant when issues of investment are minimal. This finding is consistent with suggestions that shifting preferences across the menstrual cycle may facilitate the choice of high-quality partners at peak fertility for their potential to pass genetic quality onto offspring rather than provide investment (which is minimal for short-term relationships), in line with arguments for preferences for masculinity changing across the menstrual cycle (Penton-Voak et al., 1999). Previous studies have shown that women appear to place greater emphasis on a male's physical attractiveness and physical prowess in the context of a possible short-term relationship (Buss and Schmitt, 1993). Scheib (2001) and Little et al. (2002) both show that preferences for potentially high quality but potentially un-cooperative (and potentially less committed) partners are enhanced for short-term mates. Study 1 addressed general attractiveness judgements while Study 2 highlighted that changes in preference according to fertility might be limited to short-term judgements. The results of Study 1 and 2 are not in conflict as general judgements potentially subsume a short-term component but such results do highlight that human preferences are sensitive to mating context.

In Study 2, a higher preference for male face symmetry was also seen when women where at high fertility than when they were at lower fertility if they reported having a partner but this shift did not occur for women without partners. We note, however, this was not conventionally significant. This result is inline with studies showing that symmetric men may be more likely to be chosen as extra-pair partners (Thornhill and Gangestad, 1994). Indeed, women are more likely to be interested in extra-pair mating when their partner is asymmetric (Gangestad et al., 2005), implying women may be choosing symmetric partners at peak fertility. Together, high preferences for symmetry at high fertility and in women with a partner are suggestive that symmetry is associated with a quality in a partner that is important when likely to get pregnant but when investment is unlikely to be an issue. More data is needed to confirm partnership has a significant effect on menstrual cycle shifts in preferences. Potentially the interactions between cycle and the factors addressed in Study 2 could partly explain why previous studies which do not address term or partnership have not found cycle effects on symmetry preference (Koehler et al., 2002; Oinorten and Mamanian, 2007).

Methodologically, Study 2 shows that similar results can be found in the laboratory and via the Internet. We also note the effect sizes of cyclic shifts in preferences are much larger in Study 1 than in Study 2 as individual differences in preference for symmetry will generate more noise in the between participant data, noise which is absent in within-participant tests.

9. General discussion

In line with previous studies, both studies presented here demonstrate a significant preference for facial symmetry. However, both Study 1 and Study 2 demonstrate that preferences of women for symmetry in male faces vary in relation to menstrual cycle phase. Women at high conception risk preferred more symmetric faces than those at low conception risk in both Study 1 (within-participants) and Study 2 (between-participants). These findings are consistent with cyclic preferences seen for facial masculinity (Frost, 1994; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Johnston et al., 2001) and studies showing that the smell of symmetric men is preferred at peak fertility (Gangestad and Thornhill, 1998).

Symmetric and asymmetric male faces are associated with potential costs and benefits to the reproductive success of females. Changing preference for symmetry suggests that there is some cost to choosing symmetric partners or else they would likely be preferred under all circumstances. There may be heritable immuno-competence benefits to mating with the owners of symmetric faces, as has been proposed for masculine faces, but there is a potential cost of lower paternal investment (Gangestad and Simpson, 2000; Perrett et al., 1998). It is possible that some women may choose a long-term partner whose asymmetric appearance suggests co-operation and extended paternal care and/or choose short-term partners whose higher facial symmetry may indicate better genetic quality. Females may thus trade-off heritable immunity benefits for the benefits of paternal investment. In the case of short-term mating or when a female has already acquired a long-term partner, the importance of paternal investment from a secondary partner is minimised and so females may favour male traits advertising heritable immunity benefits. Indeed, Study 2 shows that situational (current partnership status) and contextual (temporal context of the relationship) factors influence symmetry preferences in interaction with fertility. We note however that the potential three-way interaction amongst fertility, partnership and term for Study 2 was not found here.

Overall, the fluctuating preferences for symmetry seen here appear in line with what we would expect if facial symmetry advertised good-genes in males. Indeed, such strategic preferences for symmetry are problematic for views suggesting simple properties of the visual system can explain all of human preferences for symmetry (Johnstone, 1994) as such theories posit symmetry preference should be relatively constant both between and within observers (see also Little and Jones, 2003, 2006). Changing preferences for symmetry in male faces highlights the importance of flexibility in women's mate choice. While there may exist universal preferences for particular traits across populations, it appears that there are several individual differences in facial preferences that are contingent on the situation, on individual traits and on hormonal levels within an individual. Of course such strategic preference in no way implies that individuals are conscious of factors that drive their choices or that such behaviour can be considered moral.

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