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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

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Abstract

Previous studies of changes in women's behavior during the menstrual cycle have offered insight into the motivations underpinning women's preferences for social cues associated with possible direct benefits (e.g., investment, low risk of infection) and indirect benefits (e.g., offspring viability). Here we sought to extend this work by testing for systematic variation in women's preferences for male and female faces and in their attitudes to their romantic relationship during the menstrual cycle. In Study 1, we found partnered women's reported commitment to their romantic relationship and preferences for femininity in male and female faces were strongest on days of the menstrual cycle when progesterone levels are increased (and fertility is low). Happiness in relationships did not change across the cycle. In Study 2, we found that the effect of cycle phase on women's preference for feminine faces was independent of increased attraction to apparent health in faces during the luteal phase. Collectively, these findings are further evidence that women's preferences for social cues associated with possible direct benefits and commitment to relationships are strongest during conditions characterized by raised progesterone level, while attraction to men displaying cues associated with possible indirect benefits is strongest when women are most fertile.

Keywords: Menstrual cycle; Facial attractiveness; Sexual dimorphism; Progesterone

Introduction

Masculine traits in men are thought to signal heritable immunity to infectious disease and unwillingness to invest in partners and offspring (see Fink and Penton-Voak, 2002; Gangestad and Simpson, 2000 for reviews). Men's facial masculinity is positively related to their long-term health (estimated from medical records, Rhodes et al., 2003) and circulating testosterone level (Penton-Voak and Chen, 2004). In addition to possessing masculine faces, partnered men with high testosterone levels score lower on a spousal investment measure than partnered men with low levels of testosterone (Gray et al., 2002). Female attraction to masculine characteristics in male faces (Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999), voices (Feinberg et al., in review; Putz, 2004), and behavioral displays in video clips (Gangestad et al., 2004) is strongest during the late follicular phase of the menstrual cycle (when women are most fertile). It would appear that female attraction to male cues associated with possible indirect benefits (e.g., heritable immunity to infectious disease) is enhanced when fertility is high, while attraction to cues to possible direct benefits (e.g., investment) is strongest at other times. This shift in preferences may increase women's reproductive success by both increasing offspring viability and available investment

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(Fink and Penton-Voak, 2002; Gangestad and Simpson, 2000: see also Thornhill et al., 2003).

During the late follicular (fertile) phase of the menstrual cycle, women are more likely to engage in extra-pair copulations (Bellis and Baker, 1990) and sexual fantasy about men other than their primary partner (Gangestad et al., 2002) than they are during the luteal phase of the cycle. Women may increase commitment to long-term partners when in conditions similar to pregnancy (i.e., where fertility is low and progesterone level raised), but be more attracted to men possessing cues to heritable immunity to infectious disease during periods of high fertility (Fink and Penton-Voak, 2002; Gangestad and Simpson, 2000).

Aversion to facial cues associated with illness (e.g., pallor) is stronger during the luteal phase of the menstrual cycle than during the late follicular phase and stronger in pregnant women and women using oral contraceptives (which increase progesterone levels, Gilbert, 2000) than in women with natural menstrual cycles (Jones et al., 2005). Increased aversion to facial cues associated with illness that coincides with raised progesterone level (i.e., during the luteal phase, pregnancy, or following oral contraceptive use) may compensate for weakened immune system responses during pregnancy and helps maintain healthy fetal development. Increased avoidance of possible sources of contagion during pregnancy has also been observed in food preferences (Fessler, 2002; Flaxman and Sherman, 2000). As traits signaling heritable immunity to infection do not necessarily signal current condition (see Getty, 2002), hormone-mediated variation in female strategies for increasing offspring viability (e.g., changes in attraction to masculinity) and avoiding illness (e.g., changes in attraction to apparent health) might be independent. Indeed, although judgements of the masculinity and apparent health of male faces are positively related, attraction to apparent health is strongest during the luteal phase of the menstrual cycle and attraction to masculinity strongest during the late follicular phase.

Here we investigated variation among partnered women in their reported commitment and happiness with relationships and in their preferences for faces with increased masculinity (Study 1). In a different sample of women, we compared variation in women's preferences for apparent health and masculinity in faces across the menstrual cycle (Study 2). We estimated progesterone and estrogen levels from reported cycle day using published values (sensu DeBruine et al., 2005; Putz, 2004) and tested for relationships between these values and women's face preferences, reported commitment to their romantic relationship, and reported happiness in their relationship.

We tested 4 main hypothesis:

Hypothesis 1. (a) Commitment to relationships and (b) attraction to feminine male faces will be strongest on days of the cycle when progesterone levels are raised.

Putz (2004) reported that female attraction to masculine male voices was negatively related to estimated progesterone level, but not related to estimated estrogen level. We therefore hypothesized that estimated progesterone level (but not estrogen level) would be negatively related to women's preferences for masculinized faces but positively related to women's commitment to relationships. These hypotheses were tested in Study 1. Possible relationships between preferences for masculine male faces and predicted levels of estrogen and progesterone were also examined in Study 2. Indirect measures of hormone levels are appropriate for between subjects analyses as directly correlating face preferences with measured hormone levels is problematic due to the variation in average hormone levels between women.

Hypothesis 2. Attraction to feminine female faces will be enhanced on days of the cycle when progesterone level is high.

DeBruine et al. (2005) found that estimated progesterone levels were positively related to women's preferences for self-similar female faces. This may partly reflect increased preferences for associating with women who are perceived as likely to provide support during pregnancy (i.e., kin) at times when raised progesterone level prepares the body for pregnancy. As feminine female (and male) faces are perceived as 'good parents', 'trustworthy', and 'warm' (Perrett et al., 1998), estimated progesterone level might also be positively associated with preferences for femininity in female faces. This hypothesis was tested in Study 1. Johnston et al. (2001) previously found no effect of menstrual cycle phase on women's preferences for sexual dimorphism in female faces. Analysis linking preference to estimated progesterone level and with larger samples sizes could reveal menstrual cycle effects not apparent in previous studies.

Hypothesis 3. Happiness with relationships will not change during the menstrual cycle.

Increased sexual interest in men other than the primary partner during the late follicular phase of the menstrual cycle (Gangestad et al., 2002) is thought to reflect increased interest in extra pair mates (rather than seeking to replace the current mate). We therefore hypothesized that women's happiness with relationships would be relatively stable across the menstrual cycle (by contrast with their commitment to the relationship which we predict will be strongest on days of the menstrual cycle when progesterone levels are raised—see Hypothesis 1). Hypothesis 3 was tested in Study 1.

Hypothesis 4. Preferences for femininity and apparent health in faces will be independently positively related to progesterone level.

Cues signaling immunocompetence may not necessarily signal current condition (see Getty, 2002). We therefore hypothesized that preferences for apparent health and femininity in male faces would be independently positively related to predicted progesterone level. This hypothesis was

tested in Study 2. We did not predict relationships between predicted estrogen levels and face preferences.

Study 1

The aim of Study 1 was to test for relationships between partnered women's preferences for masculine male and female faces, their commitment to and happiness in their relationships, and estrogen and progesterone levels estimated from cycle day using published values.

Methods

Stimuli

Stimuli were 12 pairs of face images varying in sexual dimorphism of shape and matched in other dimensions (Fig. 1; see Perrett et al., 1998; Tiddeman et al., 2001 for methods). Each pair of faces comprised a masculine and feminine version of the same face (6 male, 6 female). In brief, masculine male and feminine female faces were manufactured by exaggerating the differences in shape between female and male face prototypes (or sample averages). Feminine male faces were manufactured by shifting the face shape towards the shape of the average female face and masculine female faces were manufactured by shifting the face shape towards the shape of the average male face. These stimuli have been used to assess masculinity preferences in previous studies (Cornwell et al., 2004; Little et al., 2001, 2002; Perrett et al., 1998; Penton-Voak et al., 1999, 2003).

Fig. 1. Male (top row) and female (bottom row) face images manipulated to increase (left) and decrease (right) masculinity of shape (sensu Penton-Voak et al., 1999; Perrett et al., 1998).

Participants

93 women (age: Mean = 25.33, SD = 2.96, range = 20–30) participated in the study. All participants described their menstrual cycles as regular and reported not using hormonal contraceptives or being pregnant. All participants were in relationships that had begun at least 3 months ago. Data from this sample of women were not analyzed in previous studies reporting effects of menstrual cycle phase on face preferences (e.g., Jones et al., 2005).

Procedure

Preferences for masculine faces were assessed using a 2 alternative forced choice task where the 12 pairs of faces were presented on screen, in a random order and interspersed with filler trials (pairs of face images that had not been manipulated in sexual dimorphism of face shape). Participants were instructed to choose the face in each pair that was most attractive. Participants reported the number of days since the onset of their most recent period of menstrual bleeding (Mean = 12.97, SD = 8.04, range = 0–31), if their menstrual cycle was regular or irregular, whether they were pregnant or using hormonal contraceptives, rated (using Likert-type scales) how happy they were in the relationship (1 = unhappy to 5 = happy), rated their commitment to the relationship (1 = uncommitted to 5 = committed), and reported if their relationship had begun between 3 and 12 months ago, between 13 months and 3 years ago, or more than 3 years ago. Responses from other participants who had indicated their relationships had lasted less than 3 months were not included in analyses because their relationships could not be considered long term. Cycle length data were not collected. In common with previous studies that have tested for individual differences in women's preferences for masculine faces (Little et al., 2001, 2002), the study was run over the internet. Participants were recruited by following links reported in New Scientist to an on-line face preference test. Duplicate entries were removed using computer ip address (see Kraut et al., 2004).

Initial processing of data

Days since last period of menstrual bleeding were converted to predicted progesterone and estrogen levels (using values from Alliende, 2002; sensu DeBruine et al., 2005). Estrogen and progesterone levels were estimated from plots of mean urinary estrone glucuronide and pregnanediol glucuronide in Alliende (2002). Values were measured using custom-programmed graph digitizing software (similar to the commercially-available "DigitizeIt").

Length of current relationship was collapsed to 2 levels (>3 years since relationship began, $N = 46$; ≤3 years since relationship began, $N = 47$). The proportion of trials (out of 6) on which feminine male faces were preferred was calculated for each participant that completed the face preference test ($N = 73$). For these women, proportion of trials (out of 6) on which feminine female faces were preferred was also calculated. These responses were converted to z-scores for comparison. Although only 73 of the women completed the face preference test, all 93 women responded to the other questions.

Results

Masculinity preferences

Preferences for femininity in male and female faces were analyzed using mixed design ANCOVA [within subject factor: sex of face (male, female); between subject factor: length of relationship (≤3 years, >3 years); covariates: age, estimated progesterone level, estimated estrogen level]. There was a significant main effect of estimated progesterone level ($F = 5.387$, $df = 1,68$, $P = 0.023$), indicating that progesterone level was positively related to preferences for femininity in both male and female faces. There was also a significant main effect of face sex ($F = 8.451$, $df = 1,68$, $P = 0.005$), indicating feminine female faces were preferred more often than feminine male faces. Although the interactions were not significant, older women tended to prefer more masculine female faces, but not more masculine male faces, than younger women ($F = 3.372$, $df = 1,68$, $P = 0.058$), and women in relationships that began ≤3 years ago tended to prefer more masculine male faces, but not more masculine female faces, than women in relationships that began >3 years ago ($F = 2.218$, $df = 1,68$, $P = 0.098$). None of the other effects were significant (all $F < 1.12$, all $P > 0.28$).

Commitment to relationship and happiness with relationship

Commitment to relationship and happiness with relationship were initially analyzed using mixed design ANCOVA [within subject factor: question (commitment, happiness); between subject factor: length of relationship (≤3 years, >3 years); covariates: age, estimated progesterone level, estimated estrogen level]. There was a significant interaction between estimated progesterone level and question ($F = 4.570$, $df = 1,88$, $P = 0.035$). Relative to women with low estimated progesterone, women with high estimated progesterone reported more commitment to their relationships, but did not differ in reported happiness with their relationships (see regression analysis below). Women in relationships that began >3 years ago were more committed to relationships and happier in relationships than women whose relationships began ≤3 years ago ($F = 4.375$, $df = 1,88$, $P = 0.038$). Women with high estimated estrogen levels also tended to report being happier in relationships and more committed to relationships than women with relatively low estimated estrogen levels ($F = 3.908$, $df = 1,88$, $P = 0.051$). There were no other significant effects (all $F < 1.270$, all $P < 0.270$).

Regression analyses were used to interpret the significant interactions revealed by ANCOVA. We first investigated the relationship between estimated progesterone level and commitment to relationship using linear regression [dependent variable: commitment to relationship; independent variables entered using the enter method: estimated progesterone level, estimated estrogen level, age, length of relationship (≤3 years, >3 years), happiness in relationship]. The overall model was significant ($F = 9.759$, adjusted $R^2 = 0.322$, $P < 0.001$). There were independent positive relationships between commitment to relationships and both estimated progesterone level ($t = 2.144$, standardized beta = 0.197, $P = 0.035$) and happiness in relationship ($t = 6.243$, standardized beta = 0.563, $P < 0.001$). There were no other significant effects (all absolute $t < 0.190$, all absolute standardized beta <0.070, all $P > 0.480$).

We investigated the relationship between estimated progesterone level and happiness in relationship in the same way [dependent variable: happiness in relationship; independent variables entered using the enter method: estimated progesterone level, estimated estrogen level, age, length of relationship (≤ 3 years, > 3 years), commitment to relationship]. Again the overall model was significant ($F = 10.400$, adjusted $R^2 = 0.338$, $P < 0.001$). Commitment to relationships and happiness in relationships were positively related ($t = 6.243$, standardized beta = 0.550, $P < 0.001$). There were no other significant effects (all absolute $t < 1.350$, all absolute standardized beta <0.125, all $P > 0.180$). These regression analyses demonstrate that the interaction between estimated progesterone level and question (revealed by the mixed design ANCOVA) was due to progesterone level being positively related to commitment to relationship and unrelated to happiness in relationship.

Study 2

In Study 2, we compared variation in women's preferences for apparent health and masculinity in male faces across the menstrual cycle. We hypothesized that attraction to apparent health and femininity in male faces would both be positively related to estimated progesterone level and that these relationships would be independent.

Methods

Stimuli

Stimuli used in Study 2 were healthy and unhealthy versions of 4 composite male face images and masculine and feminine versions of 3 of the same composite faces

(Fig. 2). Healthy and unhealthy stimuli were manufactured by transforming (see Tiddeman et al., 2001 for technical methods) each of the composite faces ± 50% of the difference in shape, color, and texture between prototypes of male faces judged by independent raters as appearing particularly healthy or particularly unhealthy (see Jones et al., 2005 for methods). Masculine and feminine stimuli were manufactured by transforming 3 of the composite faces ± 50% of the shape differences between prototypes of male and female faces (sensu Study 1 and also Little et al., 2001, 2002; Penton-Voak et al., 1999; Perrett et al., 1998).

Stimuli calibration

The 4 pairs of faces varying in apparent health and 3 pairs of faces varying in masculinity were presented on screen in a 2 alternative forced choice paradigm, in a random order, and interspersed with filler trials. Female participants (age: Mean = 24.2, SD = 3.5, range = 18–30 years, N = 33) judged the health and masculinity (in separate blocks of trials) of the stimuli by indicating which face in each of the pairs looked healthier/more masculine. The proportions of images chosen as either healthy or masculine were separately compared to chance using one-sample t tests. Faces transformed to increase masculine shape were perceived more masculine ($t(32) = 7.8$, $P < 0.001$) but not healthier ($t(32) = 0.3$, $P = 0.8$) than faces transformed to decrease masculine shape. Faces transformed to increase apparent health were judged healthier ($t(32) = 7.8$, $P < 0.001$) and more masculine ($t(32) = 4.9$, $P < 0.001$) than faces transformed to decrease apparent health. Thus, our masculinity stimuli did not contain cues to apparent health but our health stimuli contained both masculinity and apparent health cues.

Fig. 2. Examples of apparent health (top row) and masculinity (bottom row) stimuli used in the study. Composite faces were manufactured to have lowered apparent health (top row, left), raised apparent health (top row, right), increased femininity (bottom row, left), and increased masculinity (bottom row, right).

Participants

656 women (age: Mean = 24.37, SD = 2.73, range = 20–30 years) reporting no hormonal contraceptive use or pregnancy and regular menstrual cycles (cycle length: Mean = 28.79, SD = 1.105, range = 27–31 days) participated in the study. All participants reported non-UK residency. Data from this sample of women were not analyzed in Study 1 or in previous studies reporting effects of menstrual cycle phase on face preferences (e.g., Jones et al., 2005). 45.3% of the women reported having a partner.

Procedure

The 4 face pairs varying in apparent health and the 3 face pairs varying in masculinity were presented on-screen using a 2-alternative forced choice paradigm, in a randomized order, and interspersed with filler trials. Participants were told they would be shown pairs of faces and to choose the face in each pair they preferred by clicking on the options below that face. Participants indicated the extent to which they preferred a particular face by choosing from the options "guess", "slight preference", "preference", and "strong preference". Participants reported their age, hormonal contraceptive use, pregnancy status, usual cycle length, date of onset of menstrual period prior to testing, and residency. The experiment was run across the web. Participants were recruited through the BBC website by following links to an on-line study of face preferences. Duplicate entries were removed using computer ip address and similarity on an independent 16-item questionnaire (see Kraut et al., 2004).

Initial processing of data

Reported cycle length and date of onset of menstrual period prior to testing were used to calculate days until onset of next period (days until onset of next menses: Mean = 15.03, SD = 7.99, range = 0–28). These values were converted to predicted progesterone and estrogen levels using values from Alliende (2002). Responses on the face preference test were recoded using the following scale: 0 = strong preference for low apparent health/strong preference for femininity to 7 = strong preference for high apparent health/strong preference for masculinity. For each participant, the mean preference strength for apparent health (across 4 face pairs) and mean preference strength for masculinity (across 3 face pairs) were calculated and converted to percentages of maximum preference (sensu Jones et al., 2005). Percentages of maximum preferences for

apparent health and masculinity were converted to *z*-scores for comparison as different methods were used to manipulate apparent health and masculinity.

Results

Analyzing preferences by cycle phase

Preferences from the late follicular (N = 169, days until onset of next menses: Mean = 18.57, SD = 2.32, range = 15–22) and mid-luteal (N = 159, days until onset of next menses: Mean = 8.42, SD = 1.93, range = 5–12) phases were compared using mixed design ANOVA [dependent variable: % maximum preference; within subject factor: cue (masculinity, apparent health); between subject factor: phase (late follicular, mid-luteal); covariate: age]. Preferences from these phases were compared as they represent the largest difference in fertility and progesterone during the menstrual cycle (Gilbert, 2000). There was a significant interaction between phase and cue (F = 16.81, df = 1,325, $P < 0.001$) and no other significant effects (all $F < 3.1$, all $P > 0.075$). Attraction to apparent health was strongest in the mid-luteal phase of the menstrual cycle and preference for masculinity was strongest during the late follicular phase (Fig. 3). Univariate ANOVA [dependent variable: % maximum preference for apparent health; between subject factor: phase (late follicular, mid-luteal); covariates: age, % maximum preference for masculinity] confirmed that attraction to apparent health was significantly stronger in the mid-luteal phase of the menstrual cycle than during the late follicular phase (F = 6.452, df = 1,324, P = 0.012). A separate univariate ANOVA [dependent variable: % maximum preference for masculinity; between subject factor: phase (late follicular, mid-luteal); covariates: age, % maximum preference for apparent health] confirmed that attraction to apparent health was significantly stronger in the mid-luteal phase of the menstrual cycle than during the late follicular phase (F = 8.452, df = 1,324, P = 0.004).

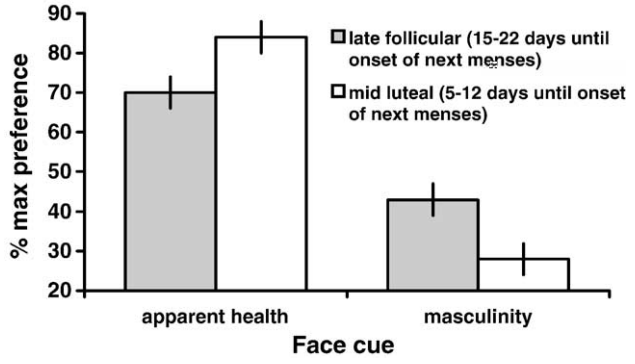

Fig. 3. The significant interaction (F = 16.81, df = 1,325, $P < 0.001$) between menstrual cycle phase (late follicular, 15–22 days until onset of next menses; mid-luteal, 5–12 days until onset of next menses) and face cue (apparent health, masculinity). While attraction to apparent health in faces was strongest during the mid-luteal phase of the menstrual cycle (when progesterone level is high and fertility is low), attraction to masculinity was strongest during the late follicular phase (when progesterone level is low and fertility is high). Bars show means and standard error. Although preferences for apparent health and masculinity were converted to *z*-scores for statistical analyses, this figure shows % maximum preferences for apparent health and masculinity.

Analyzing preferences by predicted hormone levels

To test for relationships between face preferences and hormonal changes across the menstrual cycle, preferences from all 656 women were then analyzed using ANCOVA [dependent variable: preference strength; within subject factor: cue (masculinity, apparent health); covariates: age, predicted progesterone level, predicted estrogen level]. There was a significant interaction between predicted progesterone level and cue (F = 0.336, df = 1,652, $P < 0.001$), and no other significant effects (all $F < 1.36$, all $P > 0.24$).

We used linear regression (dependent variable: predicted progesterone level; independent variables entered using the enter method: masculinity preference, apparent health preference, predicted estrogen level, age) to interpret the interaction between predicted progesterone level and face cue. The overall model was significant (F = 25.82, adjusted R^2 = 0.132, $P < 0.001$). There were independent positive relationships between progesterone and predicted estrogen level (t = 9.494, standardized beta = 0.346, $P < 0.001$) and apparent health preference (t = 2.493, standardized beta = 0.092, P = 0.013). Masculinity preference was independently negatively related to predicted progesterone level (t = −2.392, standardized beta = −0.088, P = 0.017). There was no effect of age (t = −0.883, standardized beta = −0.030, P = 0.448). The overall model in a second analysis (dependent variable: predicted estrogen level; independent variables entered using the enter method: masculinity preference, apparent health preference, predicted progesterone level, age) was significant (F = 22.754, adjusted R^2 = 0.117, $P < 0.001$). Estimated progesterone and estrogen levels were related (t = 9.494, standardized beta = 0.352, $P < 0.001$), but there were no other significant effects (all absolute values of $t < 0.5$, all standardized beta < 0.02, all $P > 0.55$).

Discussion

We found women's preferences for both feminine male (Studies 1 and 2) and female faces (Study 1) were strongest on days of the menstrual cycle when progesterone levels are raised. There were no significant relationships between preferences for sexual dimorphism in face shape and estimated estrogen level. These findings complement those of previous studies in which women were more attracted to men with masculine traits during the late follicular phase of the menstrual cycle (when fertility is high and progesterone level low) than at other times (Gangestad et al., 2004; Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-

Voak et al., 1999; Putz, 2004), and also support the proposal that cyclic variation in attraction to masculine characteristics reflects change in progesterone level (Putz, 2004). Women may obtain good genes for immunocompetence for future offspring by increasing preferences for masculine males when fertility is high. Increased attraction to feminine female faces during conditions characterized by raised progesterone level may occur because feminine women are perceived as likely to provide support during pregnancy (see DeBruine et al., 2005; Perrett et al., 1998). Alternatively, variation in preferences for feminine female faces may be a functionless (but low cost) by-product of attraction to cues to commitment or immunity in males. Although change in progesterone level appears to be more important than change in estrogen level for cyclic variation in face preferences and commitment to romantic partner, the possibility that change in other hormones, or ratios of hormones, also contributes to these shifts in behavior remains to be investigated.

Independent of the positive relationship between femininity preference and estimated progesterone level, attraction to apparent health in faces was associated with predicted progesterone level (Study 2). Attraction to masculinity was strongest during the late follicular, fertile phase of the menstrual cycle and attraction to apparent health strongest during the mid-luteal phase (Study 2). Faces with increased apparent health are rated as more masculine than faces with decreased apparent health (Study 2, Stimuli calibration), but increasing masculinity of shape does not alter attributions of health (Study 2, Stimuli calibration). Together with the significant interaction between face cue and menstrual cycle phase (Study 2), our findings for stimuli calibration suggest enhanced attraction to apparent health in the luteal phase of the menstrual cycle overrides strong preferences for feminine male faces when progesterone levels are raised. Jones et al. (2005) previously found women's preferences for apparent health in faces were enhanced during the luteal phase of the menstrual cycle and pregnancy and also in oral contraceptive users (i.e., conditions characterized by raised progesterone level, Gilbert, 2000). Increased attraction to apparent health in faces when progesterone level is raised may reduce the risk of infection during pregnancy and complements findings from studies demonstrating increased aversion to contaminated food during pregnancy (Fessler, 2002; Flaxman and Sherman, 2000). Increased attraction to apparent health in faces during conditions where progesterone level is raised does not appear to reflect an increase in drive to seek healthy long-term partners because increased attraction to apparent health when progesterone level is raised is more pronounced when male faces are judged as possible short-term partners than when male faces are judged as possible long-term partners (Jones et al., 2005). Variation in attraction to masculinity and apparent health across the menstrual cycle might be independent because traits signaling heritable immunity to infectious disease do not necessarily signal current condition (see Getty, 2002).

Women's reported commitment to relationships was strongest on days of the menstrual cycle when progesterone level is raised. Increased commitment to partner during conditions characterized by raised progesterone level may promote stable relationships during pregnancy. That reported commitment to relationships was weakest on days of the menstrual cycle when progesterone level is low is consistent with findings from previous studies where women demonstrated increased sexual interest in men other than their primary partner during the late follicular phase of the menstrual cycle compared with the luteal phase (Bellis and Baker, 1990; Gangestad et al., 2002). Although commitment to relationships was positively related to estimated progesterone level, we found no evidence for cyclic variation in happiness with relationships. The observed change in commitment to partner would therefore seem unlikely to cause women to seek to replace their long-term partners. The tendency for women with high estimated estrogen levels to rate their commitment and happiness in relationships higher than women with relatively low estimated estrogen levels may reflect a general increase in positive feelings when estrogen levels are raised (Wihlback et al., 2004).

Across the menstrual cycle, commitment to partner and attraction to facial cues associated with possible direct benefits (e.g., investment, low risk of infection) are strongest on days when progesterone levels are raised. By contrast, attraction to facial cues associated with possible indirect benefits (e.g., offspring viability) is strongest during relatively fertile conditions. Collectively, these findings are further support for the existence of adaptations whereby women in the past increased their reproductive success by increasing affiliative behavior towards people perceived as trustworthy (see also DeBruine et al., 2005), commitment to their romantic relationship (see also Gangestad et al., 2002), and contagion avoidance (see also Fessler, 2002; Flaxman and Sherman, 2000; Jones et al., 2005) during conditions characterized by raised progesterone level, and increasing attraction to more masculine men during fertile conditions (see also Gangestad et al., 2004; Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999).

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References

Alliende, M.E., 2002. Mean versus individual hormonal profiles in the menstrual cycle. Fertil. Steril. 78, 90–95.

Bellis, M.A., Baker, R.R., 1990. Do females promote sperm competition? Data for humans. Anim. Behav. 40, 997–999.

Cornwell, R.E., Boothroyd, L., Burt, D.M., Feinberg, D.R., Jones, B.C., Little, A.C., Pitman, R., Whiten, S., Perrett, D.I., 2004. Concordant

preferences for opposite-sex signals? Human pheromones and facial characteristics. Proc. R. Soc. London, B 271, 635–640.
DeBruine, L.M., Jones, B.C., Perrett, D.I., 2005. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. Horm. Behav. 47, 379–383.
Feinberg, D.R., Jones, B.C., Law Smith, M.J., Moore, F.R., DeBruine, L.M., Cornwell, R.E., Hillier, S.G., Whiten, S., Pitman, R., Perrett, D.I., in review. Average oestrogen levels predict size of menstrual cycle shifts in preferences for masculinity of male but not female voices.
Fessler, D.M., 2002. Reproductive immunosuppression and diet. Curr. Anthropol. 43, 19–61.
Fink, B., Penton-Voak, I.S., 2002. Evolutionary psychology of facial attractiveness. Curr. Dir. Psychol. Sci. 11, 154–158.
Flaxman, S.M., Sherman, P.W., 2000. Morning sickness: a mechanism for protecting mother and embryo. Quarterly Review of Biology 75, 113–148.
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. Proc. R. Soc. London, B 269, 975–982.
Gangestad, S.W., Simpson, J.A., Cousins, A.J., Garver-Apgar, C.E., Christensen, P.N., 2004. Women's preferences for male behavioral displays change across the menstrual cycle. Psychol. Sci. 15, 203–207.
Getty, T., 2002. Signaling health versus parasites. Am. Nat. 159, 363–371.
Gilbert, S.F., 2000. Developmental Biology. Sinauer, USA.
Gray, P.B., Kahlenberg, S.M., Barrett, E.S., Lipson, S.F., Ellison, P.T., 2002. Marriage and fatherhood are associated with lower testosterone in males. Evol. Hum. Behav. 23, 193–201.
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., Perrett, D.I., Little, A.C., Boothroyd, L., Cornwell, R.E., Feinberg, D.R., Tiddeman, B.P., Whiten, S., Pitman, R.M., Hillier, S.G., Burt, D.M., Stirrat, M.R., Law Smith, M.J., Moore, F.R., 2005. Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. Proc. R. Soc. London, B 272, 347–354.
Kraut, R., Olson, J., Banaji, M., Bruckman, A., Cohen, J., Couper, M., 2004. Psychological research online—report of board of scientific affairs advisory group on the conduct of research on the Internet. Am. Psychol. 59, 105–117.
Little, A.C., Burt, D.M., Penton-Voak, I.S., Perrett, D.I., 2001. Self-perceived attractiveness influences human 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.
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., Perrett, D.I., 2000. Female preference for male faces changes cyclically—further evidence. Evol. Hum. Behav. 21, 39–48.
Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, L.K., Minamisawa, R., 1999. Menstrual cycle alters face preference. Nature 399, 741–742.
Penton-Voak, I.S., Little, A.C., Jones, B.C., Burt, D.M., Tiddeman, B.P., Perrett, D.I., 2003. Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). J. Comp. Psychol. 117, 264–271.
Perrett, D.I., Lee, K.J., Penton-Voak, I.S., Rowland, D.R., Yoshikawa, S., Burt, D.M., Henzi, S.P., Castles, D.L., Akamatsu, S., 1998. Effects of sexual dimorphism on facial attractiveness. Nature 394, 884–887.
Putz, D., 2004. Women's preferences for men's voices vary cyclically with conception risk and predicted hormone levels. Paper Presented at the 15th Annual meeting of the Human Behaviour and Evolution Society. Berlin, July 2004.
Rhodes, G., Chan, J., Zebrowitz, L.A., Simmons, L.W., 2003. Does sexual dimorphism in human faces signal health? Proc. R. Soc. London, B 270, S93–S95.
Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K., Franklin, M., 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behav. Ecol. 14, 668–678.
Tiddeman, B.P., Burt, D.M., Perrett, D.I., 2001. Prototyping and transforming facial textures for perception research. IEEE Comput. Graph. Appl. 21, 42–50.
Wihlback, A.C., Poromaa, I.S., Bixo, M., Allard, P., Mjorndal, T., Spigset, O., 2004. Influence of menstrual cycle on platelet serotonin uptake site and serotonin(2A) receptor binding. Psychoneuroendocrinology 29, 757–766.