ORIGINAL PAPER: MINOT SPECIAL ISSUE

Effects of Menstrual Cycle Phase on Face Preferences

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Abstract While many studies of face preferences have emphasized high agreement among individuals about the types of faces they consider attractive and unattractive, other studies have demonstrated systematic variation in face preferences. Here, we review the evidence that women's preferences for masculinity, apparent health, and self-resemblance in faces change systematically during the menstrual cycle. Our review focuses on the proximate mechanisms that might underpin these changes (i.e., what changes in hormone levels are important for effects of menstrual cycle phase) and the possible functions of these changes (i.e., to maximize the likelihood that offspring inherit strong immune systems or to increase the likelihood of successful pregnancy by either promoting affiliation with individuals who will provide support and care during pregnancy or by promoting strategies to avoid contagion during social interactions). While evidence that differentiates between these two accounts of the function of cyclic shifts in face preferences is currently equivocal for masculinity preferences, there is compelling evidence that the function of the effects of menstrual cycle phase on preferences for apparent health and self-resemblance in faces is to increase the likelihood of successful pregnancy.

Keywords Facial attractiveness · Social perception · Mate preferences · Hormones · Menstrual cycle

Introduction

There is increasing evidence that changes in women's hormone levels during the menstrual cycle affect their social perceptions and preferences. Studies have demonstrated subtle effects of menstrual cycle phase in women with natural menstrual cycles (i.e., women not using hormonal contraceptives) on their preferences for sexual dimorphism in 2D face shape (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak et al., 1999), sexual dimorphism in 2D body shape (Little, Jones, & Burriss, 2007), apparent health (Jones et al., 2005a, b), resemblance to self in faces (DeBruine, Jones, & Perrett, 2005), and also for vocal masculinity (e.g., Feinberg et al., 2006; Puts, 2005), the odor of genetic compatibility (Wedekind, Seebeck, Bettens, & Paepke, 1995), masculine behaviors (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004), and pheromones (Grammer, 1993).

Two theories predict that women might alter their preferences during the menstrual cycle. On the one hand, women may increase attraction to men displaying putative cues to heritable immunity to infectious disease (i.e., possible indirect benefits) during ovulation, when fertility is high. On the other hand, at times when women's hormonal profile is similar to that during pregnancy or when the body is preparing for pregnancy (e.g., the luteal phase of the menstrual cycle), women may show stronger preferences for characteristics in a partner or an associate that might be beneficial at this time, such as social and material support or reduced risk of disease (i.e., direct benefits).

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Theories of attraction emphasizing good genes for immunocompetence suggest that women should make an effort to obtain a paternal genetic contribution to their offspring that maximizes offspring health (Miller & Todd, 1998; Thornhill & Gangestad, 1999). However, it may be more important for women to secure a mate with good genes for immunocompetence when they are likely to be able to use these genes (i.e., when they are likely to conceive) than at other times (Penton-Voak et al., 1999). If men with good genes for immunocompetence require a considerable amount of mating effort to obtain, or if there are tradeoffs between good genes for immunocompetence and other desirable qualities (such as willingness to invest in their offspring or partner), it would benefit women to modulate their mate preferences depending on their probability of conception (Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000). This account of the effects of menstrual cycle on preferences emphasizes the possible indirect benefits associated with mate choices (e.g., offspring inherit good genes for immunocompetence).

A different, although not mutually exclusive, theory is that the effects of menstrual cycle phase on preferences are by-products of changes in hormone levels that are associated with pregnancy or that are implicated in preparing the body for pregnancy (DeBruine et al., 2005; Jones et al., 2005a). For example, progesterone level is raised during pregnancy and raised progesterone during the luteal phase of the menstrual cycle prepares the body for pregnancy (Gilbert, 2000). Thus, effects of menstrual cycle phase on preferences and perceptions may reflect mechanisms that increase the success of pregnancy, such as strategies designed to protect the health of mother and fetus (Jones et al., 2005a, b) or strategies designed to gather social support for the mother and child (DeBruine et al., 2005; Jones et al., 2005b). Under this view, changes in preferences during the menstrual cycle would then be explainable as by-products of pregnancy-related functions. This account of the effects of menstrual cycle on preferences emphasizes the possible direct benefits associated with mate choices (e.g., increased contagion avoidance compensates for maternal immunosupression and increased preferences for kin promote support for the mother and child).

Next, we will review evidence that women's preferences for facial characteristics such as masculinity, apparent health, and self-resemblance change during the menstrual cycle. Finally, we will discuss the possible functions of these shifting preferences in light of the theories discussed above.

Masculinity

Masculine traits in men are thought to signal greater heritable immunity to infectious disease and lesser willingness to invest in partners and offspring compared to men with more feminine traits (for reviews, see Fink & Penton-Voak, 2002;

Gangestad & Simpson, 2000). Men's facial masculinity is positively related to their long-term health (estimated from medical records, Rhodes, Chan, Zebrowitz, & Simmons, 2003; estimated from incidence of colds, Thornhill & Gangestad, 2006) and circulating testosterone level (Penton-Voak & Chen, 2004; Roney, Hanson, Durante & Maestripieri, 2006). 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, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Furthermore, men with masculine faces are ascribed more negative personality characteristics (e.g., untrustworthy, cold personality) and are more dominant than men with relatively feminine faces (Mazur & Booth, 1998; Perrett et al., 1998).

Female attraction to masculine characteristics in male faces (Johnston et al., 2001; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; see Fig. 1 for examples of male faces with masculine and feminine shape characteristics), bodies (Little et al., 2007), voices (Feinberg et al., 2006; Puts, 2005), behavioral displays in video clips (Gangestad et al., 2004), and odors (Grammer, 1993) is strongest during the late follicular phase of the menstrual cycle, when women are most fertile. These effects of menstrual cycle phase on perceptions do not appear to occur in women who are using oral contraceptives (e.g., Penton-Voak et al., 1999), are most pronounced in women with partners (Penton-Voak et al., 1999), and have been observed in North American (Johnston et al., 2001), European (Penton-Voak et al., 1999), and Japanese (Penton-Voak et al., 1999) samples. Table 1 summarizes the main parameters of these studies of cyclic variation in women's preferences for facial masculinity.

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 increasing offspring viability (Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000). Women may maximize the possible benefits of their mate choices by being more open to short-term relationships with masculine men around ovulation, when fertility is highest. Consistent with this view, women generally report being more interested in socializing with men around ovulation than at other times (Haselton & Gangestad, 2006) and partnered women report more extra-pair flirtation around ovulation than at other times (Haselton & Gangestad, 2006). Furthermore, women report greater frequency of sexual fantasy about men other than their primary partner around ovulation than during the luteal phase of the cycle (Gangestad, Thornhill, & Garver, 2002). Indeed, change in preferences for masculine men during the menstrual cycle is more pronounced when women are asked to judge male faces in terms of their attractiveness for a

Fig. 1 Example of a composite male face that has been manipulated to increase (right) and decrease (left) masculinity of 2D face shape (e.g., Jones et al., 2005b; Penton-Voak et al., 1999; Perrett et al., 1998). Computer graphic methods are used to systematically and objectively alter sexual dimorphism of 2D shape in digital face images by transforming images along a continuum defined by male and female prototypes

Table 1 Summary of the main parameters of studies of cyclic variation in women's preferences for masculine faces. Number of participants refers to the number of women with natural menstrual cycles in each study (i.e. women reporting no use of hormonal contraceptives)

All of these studies showed stronger attraction to masculinity around ovulation than at other times

Study	Number of participants	Design	Measurement used to assess cycle
Johnston et al. (2001)	42	Within-subjects	Diary
Jones et al. (2005b, Study 1)	93	Between-subjects	Diary
Jones et al. (2005b, Study 2)	656	Between-subjects	Diary
Penton-Voak et al. (1999, Study 1)	39	Within-subjects	Diary
Penton-Voak et al. (1999, Study 2)	43	Within-subjects	Diary
Penton-Voak and Perrett (2000)	139	Between-subjects	Diary
Welling et al. (2007)	70	Within-subjects	Diary and salivary testosterone

short-term relationship (e.g., an affair) than when women are asked to judge male faces in terms of their attractiveness for a long-term relationship (e.g., marriage) (Johnston et al., 2001; Penton-Voak et al., 1999). Welling et al. (2007) recently found that women's preferences for masculine faces were strongest on days of the menstrual cycle when levels of salivary testosterone were high, suggesting change in testosterone level may be an important hormonal mechanism for cyclic changes in women's masculinity preferences. Since raised testosterone is associated with both increased sex drive (Riley & Riley, 2000) and ovulation (Alexander, Sherwin, Bancroft, & Davidson, 1990; Bloch, Schmidt, Su, Tobin, & Rubinow, 1998), Welling et al.'s findings are consistent with the view that increased attraction to masculine men around ovulation may function to increase offspring health.

While most studies of the effects of menstrual cycle phase on masculinity preferences have emphasized the possible indirect (i.e., genetic) benefits of increased attraction to masculine men around ovulation (e.g., Johnston et al., 2001), recent findings have also suggested that the effect of menstrual cycle phase on preferences for masculine men may, at least partly, reflect

increased attraction to possible sources of care and support when raised progesterone prepares the body for pregnancy (i.e., direct benefits).

Jones et al. (2005b) found that women's preferences for femininity in both male and female faces changed during the menstrual cycle. Preferences for femininity in female and male faces were stronger during the luteal phase of the menstrual cycle than at other times, and the change in preference for femininity was positively related to the estimated change in progesterone level. Because feminine female and male faces are perceived as more trustworthy and "better parents" than their masculine counterparts are (e.g., Perrett et al., 1998), Jones et al. (2005b) suggested that increased attraction to feminine individuals at times when the body is preparing for pregnancy may increase the amount of support women receive during pregnancy. Puts (2006) found that increased attraction to relatively feminine voices during the luteal phase was also positively related to the estimated change in progesterone level. Jones et al.'s findings demonstrating increased preferences for feminine men *and* women during the luteal phase of the menstrual cycle that is positively related to the estimated change in

progesterone level point to a different (but not mutually exclusive) possible explanation of changes in women's preferences for masculine individuals during the menstrual cycle whereby attraction to femininity increases the care and support that is available during pregnancy.

Many studies have demonstrated systematic variation in the magnitude of cyclic shifts in women's masculinity preferences. For example, cyclic shifts in women's masculinity preferences appear to be most pronounced in women with romantic partners (Penton-Voak et al., 1999). Additionally, feminine women, as indexed by responses on a test of sex-typical attitudes (Johnston et al., 2001) or by late-follicular phase estrogen level (Welling et al., 2007) showed larger cyclic shifts in attraction to masculinity in men's faces than did relatively masculine women. However, Feinberg et al. (2006) found that women with high average levels of estrogen showed smaller cyclic shifts in attraction to masculine voices than did women with relatively low average levels of estrogen. This finding was interpreted as potentially indicating that feminine, high-quality women are better able to obtain investment from masculine, high-quality men. Individual differences in the magnitude of cyclic shifts in women's mate preferences remains an important topic for future research. In particular, it is intriguing that feminine women appear to show bigger cyclic shifts in attraction to masculine faces, but show smaller cyclic shifts in attraction to masculine voices. This could indicate that the functions of cyclic shifts in preferences for facial and vocal masculinity are not identical.

Apparent Health

Jones et al. (2005a, b) investigated the effect of menstrual cycle phase on women's preferences for faces varying in health of appearance (e.g., color and texture cues associated with high and low apparent health). Table 2 summarizes the main parameters of these studies. Aversion to faces with cues associated with illness (e.g., pallor) was stronger during the luteal phase of the menstrual cycle (when progesterone level is raised and fertility is low) than during the late follicular phase (when progesterone level is low and fertility is high). This effect was observed for judgements of the attractiveness of both male and female faces, and was more pronounced when male faces were judged in terms of their attractiveness as a partner for a short-term relationship than when male faces were judged in terms of their attractiveness as a partner for a long-term relationship (Jones et al., 2005a). Furthermore, change in attraction to faces with high apparent health appeared to reflect estimated change in progesterone level during the menstrual cycle: estimated progesterone level was positively related to the strength of preferences for faces with high apparent health, but estrogen level was not related to the strength of preferences for faces with high apparent health (Jones et al., 2005b). While previous studies relied exclusively on self-reported cycle data to assign test days to different cycle phases, these studies used a combination of self-reported diary data and measured progesterone levels from urine samples.

Importantly, the effect of menstrual cycle phase on health preferences was observed in a sample of women who showed a general preference for masculine faces and increased attraction to masculine faces around ovulation (Jones et al., 2005b), establishing that increased attraction to health during the luteal phase of the menstrual cycle is not an artefact of women demonstrating stronger face preferences in general during the luteal phase of the menstrual cycle than at other times. Change in preferences for male faces manipulated in apparent health were independent of change in preferences for masculine faces, indicating that the effect of cycle phase on health preferences was not a by-product of change in preferences for masculinity (Jones et al., 2005b).

Because change in women's preferences for faces varying in health of appearance was associated with change in progesterone level during the menstrual cycle, and because progesterone level is also raised during pregnancy and following use of most oral contraceptives (Gilbert, 2000), Jones et al. (2005a) also investigated the effects of pregnancy and oral contraceptive use on health preferences. Women who were pregnant reported stronger preferences for faces with high apparent health than

Table 2 Summary of the main parameters of studies of variation in women's preferences for apparent health in faces

Study	Number of participants	Design	Measurement used to assess cycle
Jones et al. (2005a, Study 1)	639	Between-subjects	Diary
Jones et al. (2005a, Study 2)	19	Within-subjects	Diary and urinary progesterone
Jones et al. (2005a, Study 3)	22	Within-subjects	Diary and urinary progesterone
Jones et al. (2005a, Study 4)	115 (pregnant), 857 (natural cycles)	Between-subjects	N/A
Jones et al. (2005a, Study 5)	1570 (oral contraceptive users), 1325 (natural cycles)	Between-subjects	N/A
Jones et al. (2005b, Study 2)	656	Between-subjects	Diary

Number of participants refers to the number of women with natural menstrual cycles in each study (i.e. women reporting no use of hormonal contraceptives) unless stated otherwise. All of these studies showed stronger attraction to apparent health during the luteal phase than during the late follicular phase of the menstrual cycle, except for Jones et al. (2005a) studies 4 and 5 which showed stronger attraction to apparent health in pregnant women and women using oral contraceptives than in women with natural menstrual cycles

women with natural cycles who were matched in terms of age, partnership status, and country of residency. Furthermore, women using oral contraceptives demonstrated stronger preferences for apparent health in faces than did women with natural cycles when possible effects of partnership status, age and country of residency were controlled for in analyses.

Collectively, these findings indicate that preferences for apparent health in faces are strongest during conditions associated with raised progesterone level (e.g., pregnancy, luteal phase of the menstrual cycle, and following oral contraceptive use). Increased aversion to facial cues associated with illness at these times may reflect a mechanism that compensates for maternal immunosupression by reducing the likelihood of women contracting illnesses during social interactions and that protects the developing fetus. Indeed, increased aversion to possible sources of illness during pregnancy has also been observed in food preferences during pregnancy (Fessler, 2002; Flaxman & Sherman, 2000). Moreover, raised salivary progesterone during the menstrual cycle is also associated with increased salience of facial cues to nearby danger and contagion (Conway et al., 2007). It is unlikely that increased aversion to male faces with cues associated with illness at times when progesterone level is raised reflects increased attraction to healthy men who may provide durable care and investment as long-term partners during pregnancy or when the body is preparing for pregnancy because change in health preference during the menstrual cycle was more pronounced when male faces were judged as a possible short-term partner than a long-term partner.

Self-Resemblance

Cues of kinship can signal both increased direct benefits, in the form of altruism from family members, and decreased indirect benefits, in the form of inbreeding depression. Women may show cyclic changes in their preferences for cues of kinship for one or both of these reasons. That is, women may show aversions to potential mates displaying kinship cues near ovulation, when the cost of an incestuous mating is highest, or they may increase their preference for kinship cues when raised progesterone prepares the body for pregnancy.

One potential cue of kinship is similarity of the major histocompatibility complex (MHC). Since genetic relatives tend to share many of the same alleles in the MHC, inbreeding causes the number of distinct alleles in the MHC to decrease, weakening immune function (Penn & Potts, 1999). Preferences for MHC similarity have been shown to vary with pregnancy status in mice and hormonal state in humans. Although female mice tend to prefer mates with dissimilar MHC odor signatures (Penn & Potts, 1998), pregnant mice prefer to nest with others who share their MHC odor (Manning, Wakeland, & Potts, 1992). Human women using oral contraceptives that mimic the

effects of raised progesterone during pregnancy demonstrate stronger preference for self-similar MHC odors than do women with natural cycles (Wedekind et al., 1995). Other cues of kinship may also be preferred when women's hormonal profile is similar to that of pregnancy.

Facial resemblance to self is a cue that humans respond to in a manner consistent with it being a cue of kinship (see DeBruine, Little, Perrett, & Jones, 2008). While kin tend to be favored in most social contexts, some cues of kinship (e.g., early close association, Westermarck, 1921) are unattractive in a mating context. Consistent with this, both men and women judge self-resembling other-sex faces to be particularly trustworthy but unattractive, especially when judging the attractiveness of other-sex faces for a short-term relationship (DeBruine, 2005), where the costs of inbreeding cannot be offset by benefits such as greater duration of marriage and extended family support for a large family size (Bittles, Grant, Sullivan, & Hussain, 2002).

To test if preferences for self-resembling faces vary across the menstrual cycle and whether this functions to decrease the genetic costs of inbreeding when women are most fertile or to motivate kin-seeking behaviors during pregnancy, DeBruine et al. (2005) tested women's (N = 74) preferences for self-resembling male and female faces at different points in the menstrual cycle. Preferences for self-resemblance were greater during the non-fertile luteal phase than during the fertile late follicular phase. Correlational analyses determined that preferences for self-resemblance were positively associated with progesterone levels (as estimated from reported cycle day), but not with estrogen levels or conception risk. In addition, these effects were stronger for female faces than for male faces, leading to the conclusion that cyclic shifts in preference for self-resemblance function to motivate seeking support from kin rather than preventing inbreeding.

Discussion

In terms of whether the effect of menstrual cycle phase on women's preferences for facial masculinity reflects increased attraction to facial cues which, in men, are associated with possible indirect benefits (e.g., offspring inherit strong immune systems) or facial cues associated with possible direct benefits which will increase the success of pregnancy (e.g., greater amounts of care and support), evidence is equivocal. On the one hand, increased attraction to masculine men during the late follicular phase of the menstrual cycle is more pronounced when men are judged for a possible short-term relationship than when men are judged as possible long-term partners. This latter finding supports the proposal that the function of the effect of menstrual cycle phase on preferences for masculinity is to increase offspring health by increasing women's willingness to mate with masculine partners when fertile (e.g., Johnston et al.,

2001; Penton-Voak et al., 1999). On the other hand, increased preferences for femininity during the luteal phase of the menstrual cycle, when raised progesterone prepares the body for pregnancy, has been observed for judgements of both male and female faces and was related to change in progesterone level. This supports the view that the function of the effect of menstrual cycle phase on preferences for masculinity is to promote affiliation with individuals who will provide support and care during pregnancy (Jones et al., 2005b). Of course, these two accounts of the effect of menstrual cycle phase on masculinity preferences are not necessarily mutually exclusive: the function of cyclic changes in attraction to masculinity may be both to increase offspring health *and* to promote affiliation with individuals who are likely to be valuable sources of care and support during pregnancy.

While evidence that differentiates these two accounts of the function of the effects of menstrual cycle phase on preferences for masculine faces is equivocal, there is compelling evidence that the function of the effects of menstrual cycle phase on preferences for apparent health and self-resemblance in faces is to promote the success of pregnancy. Attraction to apparent health in male and female faces is stronger during the luteal phase of the menstrual cycle than during the late follicular phase and appears to reflect change in progesterone level (Jones et al., 2005b). Furthermore, attraction to apparent health in faces is stronger in pregnant women than in women with natural menstrual cycles (Jones et al., 2005a). These findings support the proposal that increased attraction to apparent health when women are in conditions that are characterized by raised progesterone levels reflect a mechanism that reduces the likelihood of pregnant women contracting illnesses during social interactions (Jones et al., 2005a, b). That preferences for self-resemblance are stronger during the luteal phase of the menstrual cycle than during the late follicular phase, particularly when judging female faces for which attraction carries no possible cost of inbreeding, and are correlated with change in progesterone level rather than conception risk, suggest that the function of the effect of menstrual cycle phase on preferences for self-resemblance in faces is to promote affiliation with individuals who are likely to provide care and support during pregnancy, rather than to avoid inbreeding at times when the costs of inbreeding are particularly pronounced (DeBruine et al., 2005).

Although it is well established that face preferences influence many different social outcomes (e.g., partner and associate choices, hiring decisions, and voting behavior, see Langlois et al., 2000), most studies of face preferences have focused on identifying facial characteristics that are generally attractive (i.e., characteristics that are, on average, preferred by people). The findings for effects of menstrual cycle phase on women's preferences for masculinity, apparent health, and self-resemblance in faces that were reviewed here contribute to a growing literature demonstrating that variation in face

preferences is systematic. Although the precise nature of the functions of hormone-mediated face preferences remains somewhat unclear, they do appear to evince adaptive design in female mate preferences.

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