

Women's Probability of Conception Is Associated with their Preference for Flirtatious but not Masculine Facial Movement

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Abstract Women's preferences for facial structure vary over the menstrual cycle. Little is known, however, as to how preferences for behavior may be influenced by hormonal factors. Here, we demonstrate that social properties of facial motion influence attractiveness judgments in the absence of other cues, and that women's preferences for these displays vary over the menstrual cycle, as has been demonstrated for structural traits of men's faces in static stimuli. We produced shape-standardized facial models that were animated with male movement and assessed for flirtatiousness by 16 women and attractiveness by 47 women. In fertile phases of the menstrual cycle, women showed stronger preferences for flirtatious movement, but not for absolute movement. These data show that women (1) recognize specific mating-relevant social cues in male facial movement and (2) are differentially influenced by these cues at different phases of the menstrual cycle. This preference for flirtatiousness may promote the adaptive allocation of mating effort towards men who are, in turn, likely to respond positively.

Keywords Facial attractiveness · Facial movement · Dynamic stimuli · Mate choice · Menstrual cycle · Flirting

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Introduction

In humans, sexual intercourse can only result in pregnancy in the late follicular phase around ovulation. Several changes have been documented in women's behaviors and preferences over the menstrual cycle that, functionally, seem adaptive in light of this short window of fertility. During the follicular phase, women are more likely to go out to places where they can meet men (Haselton & Gangestad, 2006) and make themselves more attractive through grooming, ornamentation, and dress (Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007). Women's gait also changes over the menstrual cycle (Provost, Quinsey, & Troje, 2008a). Furthermore, at these times, women particularly prefer taller men (Pawlowski & Jasienska, 2005), deeper male voices (Feinberg et al., 2006), and the odor of more symmetrical men (Gangestad & Thornhill, 1998) (for a review, see Gangestad & Thornhill, 2008). Sexually dimorphic or symmetrical traits are recognized throughout nature as signaling heritable quality in males (Andersson, 1994; Møller & Thornhill, 1998) and, by preferring them when fertile, females increase the chances of passing them on to their offspring hence increasing their own reproductive success. Cyclic shifts have also been documented for women's preferences for male faces. During the fertile window, women prefer more masculine faces than they do at other times of the month (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Jones et al., 2005b; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Scarbrough & Johnston, 2005). Additionally, one recent study has found a cyclic preference for facial symmetry in humans, which may be a correlate of facial masculinity (Little, Jones, Burt, & Perrett, 2007).

To date, most studies of menstrual cycle shifts in preferences have concentrated on traits that are sexually dimorphic (height, voice pitch, facial structure) and hence potentially indicate heritable biological quality. All three of these traits

are associated with testosterone (Dabbs & Mallinger, 1999; Heald et al., 2003; Penton-Voak & Chen, 2004), which is itself thought to be an honest signal of immunocompetence (Folstad & Karter, 1992), although this link lacks direct empirical support to date. The logic behind this so-called “good genes” argument is that preferences evolve for traits that honestly signal mate quality. This quality is to some extent heritable, and can be passed on to offspring, thereby improving reproductive success. In humans, mate quality has many components, but considerable research has concentrated on the possibility that attractiveness may be associated with developmental health, a key aspect of biological quality. There is some evidence for this link (e.g., Hume & Montgomerie, 2001; Langlois et al., 2000; Zebrowitz & Rhodes, 2004). Interestingly, men with attractive faces are more heterozygous at tested loci within the major histocompatibility complex, which is important for immune function (Roberts et al., 2005). Signals to good genes, however, may indicate costs as well as benefits. Although facial masculinity may indicate biological quality, it also drives negative personality attributions, such as coldness and dishonesty (Perrett et al., 1998), and signals less willingness to invest in offspring (Roney, Hanson, Durante, & Maestripieri, 2006). A masculine male may, therefore, represent a high-quality but high-risk mate who offers good genes but less investment than a less masculine male. In the context of these conflicting cues, ovulatory shifts in preferences are often proposed to result from females “trading off” traits desirable in long-term and short-term partners (paternal investment and good genes, respectively) depending on the chance of conception (Gangestad & Thornhill, 2008).

Women, however, may also profit from attending to traits in addition to those associated with “good genes.” Cues or signals that indicate a likely return on mating effort may also be preferred, irrespective of the relationship between such cues and traits associated with good genes. Mating effort is costly in terms of time, energy, and resources, and individuals should minimize wasted effort if they are limited by any of these factors. Flirting may signal to both men and women an increased probability of reward for mating effort invested (Mishra, Clark, & Daly, 2007). Although females are usually construed as choosy and males as indiscriminate throughout nature, humans are a largely monogamous species which may select for substantial male choice (Johnstone, Reynolds, & Deutsch, 1996; Kenrick, Sadalla, Groth, & Trost, 1990). A flirting man may, therefore, be signaling interest to a woman, and this cue would be especially valuable to women time-constrained by windows of fertility.

Behavioral cues, such as flirtatiousness, are an important component of attractiveness, but few studies have examined them. Although dynamic mating displays are well-studied in other species (e.g., Bakker, Künzler, & Mazzi, 1999; May-

nard Smith, 1956; Rowland, 1995), most facial attractiveness research in humans has relied on photographs or photographic composites. Flirtatious displays are difficult, if not impossible, to study with static stimuli because they are often dynamic by nature, and recent studies indicate that the attractiveness of the same face in a static photograph and a dynamic video do not necessarily correlate (Lander, 2008; Penton-Voak & Chang, 2008; Rubenstein, 2005). Flirtatious displays may also be linked to good genes in humans, although this idea is speculative. Simpson, Gangestad, and Biek (1993) found that symmetrical men engaged in different courtship tactics than asymmetrical men. It is worth noting that testosterone is associated with both anatomical and behavioral displays in a wide variety of species (Adkins-Regan, 2005). In birds, for example, testosterone treatment can restore castrated cockerels’ crowing and sexual behavior and can even bring female canaries into song (for a review, see Fusani, 2008). The possibility that preferences for dynamic behavioral traits are influenced by menstrual cycle phase has received little research attention. Gangestad, Simpson, Cousins, Garver-Apgar, and Christensen (2004) did examine preferences for videotaped behavioral displays, showing that women’s preferences for directly competitive courtship behavior were heightened during fertile phases of the menstrual cycle when the men were being judged as potential short-term, but not long-term, partners. Here, directly competitive courtship behavior was defined from factor analysis of men’s behavioral tactics and nonverbal behaviors to include things like derogation of a male competitor, asserting their own superiority, and lack of laughing. That study, however, was not concerned with examining the dynamic aspects of the behavior alone, as video footage contained both dynamic and structural cues (although there was an attempt to statistically control for static face attractiveness in this study, there were potential interactions between dynamic and static cues that could not be controlled by these means).

In order to investigate dynamic cues, it is useful to isolate them from potential confounding variables. Motion capture is an important tool in this respect and can provide a clear insight into the importance of motion itself in attractiveness judgments in humans. For example, Brown et al. (2005) used motion capture to demonstrate an association between body symmetry and dance quality. Morrison, Gralewski, Campbell, and Penton-Voak (2007) used a form of motion capture to examine facial dynamics and showed that sex-typical facial motion in females was rated attractive by males and females. In this study, however, sex typical (i.e., masculine) facial movement was not related to attractiveness for male targets, yet both male and female raters agreed on the male faces that were attractive based on their movement, suggesting that some (as yet unidentified) quality or qualities in male facial movement drive attractiveness judgments.

In the current study, we investigated whether women's preferences for two properties of facial movement varied over the menstrual cycle. First, we assessed whether preferences for sex-typicality in facial movement varied in a similar way to the well demonstrated shifting preferences for structural masculinity. Such an effect has recently been demonstrated by Provost, Troje, and Quinsey (2008b), who isolated the biological motion of walkers, showing that fertile women particularly preferred masculinity in shape-controlled point-light displays. The large anatomical differences in, for example, pelvic structure, lead to easily observable sex differences in walking style. Although anatomical constraints that lead to sex differences in facial movement are less obvious than in gait, there are nevertheless reliable cues to sex in facial movement alone (Hill & Johnston, 2001; Morrison et al., 2007). If preferences for masculinity in facial movement are analogous to preferences for masculinity in the structural properties of faces and the dynamic properties of gait, we should expect preferences for masculine movement to be highest in the follicular phase of the menstrual cycle.

Secondly, we assessed whether preferences for flirtatious facial movement, which signals likely reward for mating effort, is more important to women when their conception probability is high. To test these ideas, we measured women's preferences for flirtatious dynamic facial displays as a function of their likelihood to conceive following intercourse, using actuarial data from an earlier study (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). Conception probability is a useful variable when investigating the adaptiveness of menstrual shifts in behavior and preferences. The mechanism behind such shifts is presumed to be hormonal, and there is evidence that women's facial preference shifts are associated with days of the menstrual cycle when levels of estrogen (Jones et al., 2005a) and progesterone (DeBruine, Jones, & Perrett, 2005) are predicted to be high. We specifically investigated women's preferences for short-term attractiveness judgments, as menstrual cycle effects are particularly predicted in this context (e.g., Jones et al., 2005b; Penton-Voak et al., 1999).

Method

Participants

Facial Animations

Facial animations were the same as those in Morrison et al. (2007). Briefly, we obtained facial motion data from 1-min video sequences of five men in conversation with an interviewer about their upcoming Christmas holidays. These men were young, Caucasian undergraduates recruited at Stirling University.

Flirtatiousness Ratings

Participants were 16 psychology students who received course credit for participation.

Attractiveness Ratings

A further set of 47 women (M age = 19.8 years), none of whom were taking the contraceptive pill, rated the same animations.

Procedure

Facial Animations

Facial landmark points were labeled semi-automatically with 30 points per frame. The movement of these points was then transferred to an androgynous line face and then split into sequences of 10 s, resulting in 30 clips. For further technical details of these computer graphic techniques, see Gralewski, Campbell, Morrison, and Penton-Voak (2006). For each 10 s clip, the total amount of movement was estimated by calculating the distance travelled by the centroid point (the imaginary point representing the average spatial position of each landmark) across each frame of the sequence ($M = 261$ pixels, $SD = 50.1$; Morrison et al., 2007). This earlier study also provided a masculinity score for each clip, which was the number of times a given clip was correctly identified as male in the previous study. Here, 108 raters (68 female, 40 male) viewed the 30 male clips in the current study and 30 female clips constructed using identical techniques in random order, and decided whether each was male or female (M of male clips = 65.8/108 possible male identifications, $SD = 7.5$, no sex of rater effects, see Morrison et al., 2007, for full details of this study). The study was approved by the ethics committee of the Department of Experimental Psychology, University of Bristol.

Flirtatiousness Ratings

Participants viewed the animations in random order and rated the flirtatiousness of each clip from 1 (not very flirtatious) to 7 (very flirtatious).

Attractiveness Ratings

Participants viewed the same clips in random order and rated their short-term attractiveness on a 1 to 7 scale. Participants were given the following definition: "By 'short-term attractiveness,' we refer to the type of person who would be attractive to you in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur

of the moment, an affair within a long-term relationship, or the possibility of a one-night stand.” All participants were aware that they were viewing male faces.

Women were asked how many days it had been since the onset of their last period, and from this we calculated each participant’s probability of conception from a single act of unprotected intercourse using benchmark data from Wilcox et al. (2001), who provided 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.

Measures

Inter-rater agreement for the flirtatiousness ratings was high (Cronbach’s $\alpha = 0.79$). We therefore averaged the ratings, giving each clip a single flirtatiousness score ($M = 4$, $SD = 0.95$). We were interested in the relationship among flirtatiousness, masculinity, and attractiveness of the clips, and the influence of the menstrual cycle on this relationship, and performed simple correlations to assess these associations. To assess individual participant’s preferences for flirtatiousness, we performed a median split on the animations to divide them into the 15 most flirtatious and the 15 least flirtatious. We then averaged each woman’s attractiveness ratings for the animations in these groups to give her two scores. The difference between each woman’s average for the high flirtatiousness and low flirtatiousness groups represented her “preference for flirtatiousness.” We then repeated this procedure for a median split on masculinity to calculate each woman’s “preference for masculinity.” For use as a control measure, we also calculated a “preference for movement” score in the same way using a median split on the total amount of movement in each of the 30 clips.

One potential weakness with simple correlations is that data must be aggregated to create the dependent variables. We therefore performed another analysis involving hierarchical linear modeling, which allows each individual rating to be included by nesting each rating within each female rater. This approach also allowed us to consider the effects of flirtatiousness, masculinity, and movement simultaneously because all three are included in a regression equation for each rater. Another advantage is that hierarchical modeling can test for main effects of conception likelihood, i.e., do women give higher or lower ratings generally when fertile? Hierarchical linear modeling is a form of regression in which some data at one level share error terms and hence are not independent. This shared variance can be taken into account by organizing the related Level 1 data under Level 2 units of analysis. At Level 1 of our model was the relationship between flirtatiousness, total movement, and masculinity of each clip as independent variables and the individual woman’s attractiveness rating of that clip as the dependent

variable. Thus, there was a population of regression slopes each representing one woman’s ratings. Level 2 of the model examined the effect of the rater variable—each woman’s probability of conception—on the intercept and slope of the regression lines. All p -values are two-tailed.

Results

Conception Probabilities

Using data from Wilcox et al. (2001; Table 1, column 1, estimated mean probability of pregnancy of following a single act of unprotected intercourse), we estimated that the mean probability of conception of participants when tested in our study was 2.7% ($SD = 3.0\%$; range, 0–8.6%). In the late follicular phase (days 7–15), this value was 4.8% ($SD = 2.9\%$, $n = 19$), and the combined conception probability during menses (days 1–6, $n = 14$) and the luteal phase (days 16–29, $n = 14$) was 1.3% ($SD = 2.1\%$). These values were significantly different $t(45) = -4.9$, $p < .001$. These data are as would be expected from a random sample of naturally cycling women. Wilcox et al. (2001) also split their sample to provide conception probability data for women with regular and irregular cycles. Substituting either of these additional data sets for the combined data in our analyses had no influence on the pattern or significance of any effects.

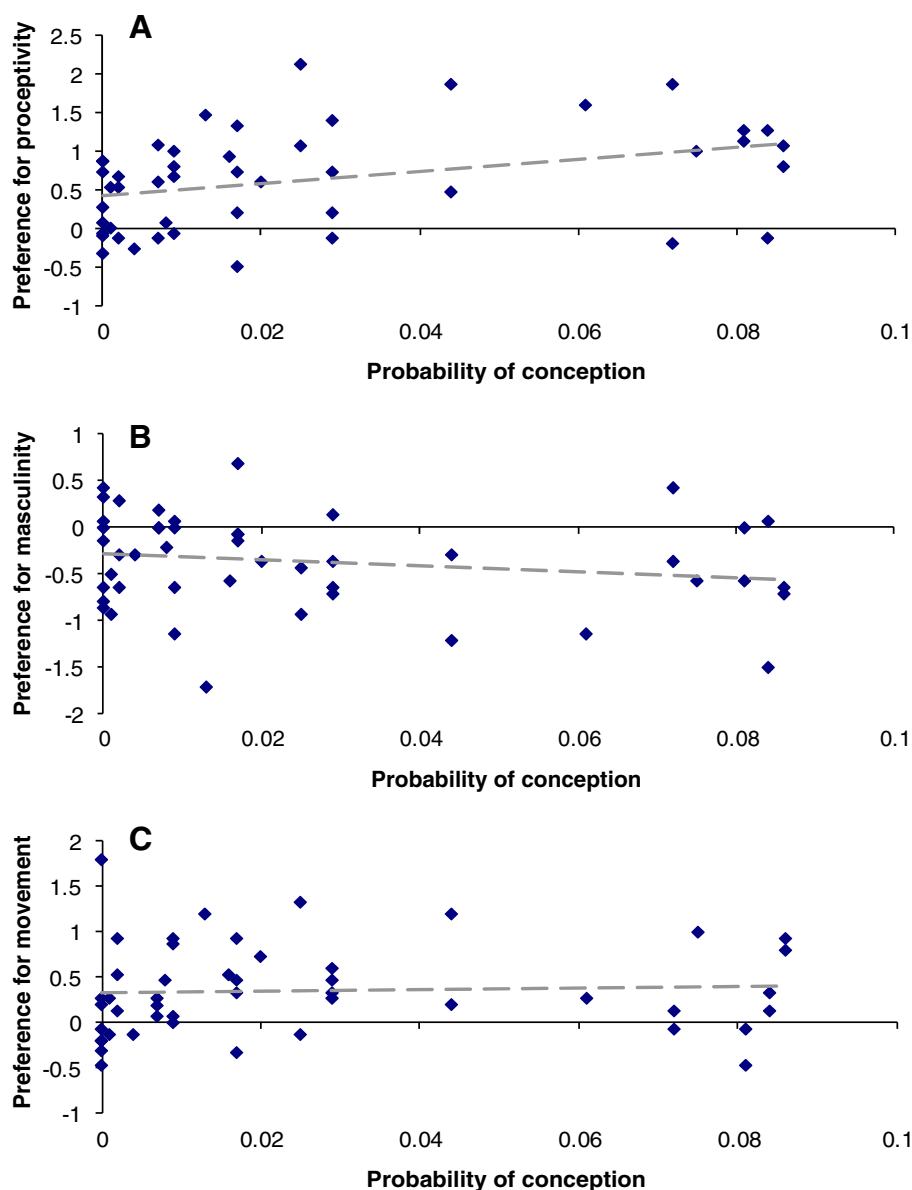
First Order Correlational Analysis

To assess whether conception probability was associated with preferences for flirtatiousness, masculinity, and total movement, we performed two Spearman’s nonparametric correlations. The correlation between flirtatiousness preference and conception likelihood was positive and significant ($r_s = .44$, $p = .002$, $n = 47$). There was no significant association between the probability of conception and preference for masculinity ($r_s = -.19$, $n = 47$) or preference for overall movement in the clips ($r_s = .22$, $n = 47$). See Fig. 1 for scatterplots of these relationships.

Hierarchical Regression Analysis

In our hierarchical model, the slopes of the Level 1 relationship represented each woman’s preference for flirtatious movement, masculine movement, or total amount of movement. The steepness of the flirtatiousness slopes was positively associated with each woman’s probability of conception, $\gamma = 0.10$, $t(45) = 2.01$, $p = .043$, meaning that when more fertile, women found flirtatious faces especially attractive. The intercepts of these slopes were not affected by probability of conception, $\gamma = 0.10$, $t(45) = 1.42$, $p = .16$, meaning that women did not give higher or lower ratings overall

Fig. 1 Associations between the conception probability for flirtatious movement (Panel A), masculine movement (Panel B), and total movement in dynamic male faces (Panel C)



when fertile. There were no such effects for women's preference for masculinity ($\gamma = -0.02, t(45) < 1$), or movement ($\gamma = -0.05, t(45) = -1.24$).

Flirtatious animations were attractive generally, as evidenced by a main effect at Level 1 in the model, $\gamma = 0.24, t(45) = 6.10, p < .001$. This result would be unsurprising if it were just the result of a halo effect whereby those animations that moved more were rated more attractive (as in Morrison et al., 2007) and more flirtatious. But this was not the case, since the model also included and controlled for the amount of movement in each animation. Masculinity was negatively associated with flirtatiousness ($r_p = 0.40, n = 30, p = .03$), but this relationship disappeared when controlling for the amount of movement in each clip (partial correlation $r = -0.10, df = 27$). The intraclass correlation coefficient for the null model was 0.23, meaning that 23% of the

variances in attractiveness ratings could be attributed to differences between the raters.

Discussion

Our data showed that women's preference for flirtatious facial movement increased at times of the menstrual cycle when they are more likely to conceive following intercourse. This finding was consistent with a growing body of evidence that female preferences for men's traits undergo menstrual cycle shifts, but was the first to examine facial movement independently of structural cues. Interestingly, the same menstrual shift was not apparent in terms of women's preference for the amount of movement in faces. Women did not seem to be merely responding to a low level perceptual variable like

amount of movement. Instead, participants were differentially responding to the social value of the signal.

We found no evidence that women's preferences shifted towards masculine motion when they are fertile. This is at odds with findings using both static faces (e.g., Penton-Voak et al., 1999) and whole-body motion (Provost et al., 2008b). With static faces, masculinity is defined in a variety of ways, but all relate to either measured or perceived sex differences in facial shape (for a discussion of these methods, see DeBruine et al., 2006), which are in turn related to hormone levels (Penton-Voak & Chen, 2004; Pound, Penton-Voak, & Surridge, 2009). For the Provost et al. (2008b) stimuli, masculinity denoted sex differences in motion identified from Fourier analysis of point-light walkers and principal components analysis. Hormones affect body morphology and hence presumably gait, although this link is not directly established. In our case, masculinity was operationalized simply by identifying how often each dynamic clip was identified as male in a forced choice decision task, and no direct link between endocrine activity and facial movement has been hypothesized or established. It is possible that this difference in definition accounts for our lack of a finding, but in this context it is worth noting that most alternative methods of estimating static face masculinity show strong relationships to each other and outcome variables of interest (DeBruine et al., 2006). A more likely explanation may lie in the differences in social attributions made to static and dynamic masculinity. Although masculine facial structure is often attributed with negative personality attributions of coldness and dominance, it is also associated with some stereotypically attractive features, such as a prominent jaw line. Unlike masculinity in static faces, masculine movement is not readily associated with any positive features, as the major sex difference in facial movement is one of degree, with males moving their faces less than women overall (Morrison et al., 2007). This idea was supported by our finding that flirtatious and masculine movement were negatively correlated, but this relationship was mediated by the amount of movement. The relative lack of absolute movement found in our "masculine" dynamic displays (in the operationalization of masculinity we used here) may not signal biological quality so much as a social disengagement, which is unlikely to be considered attractive in any context.

Our definition of masculinity was based on social perception rather than rated masculinity (asking participants how masculine each clip looked) or the mathematical differences between male and female movement (e.g., based on Fourier analysis). This is to allow comparison with the results of Berry (1991) and Hill and Johnston (2001). Rated masculinity is also subjective and may be prone to halo effects based on attractiveness, and although a Fourier-based analysis of sex differences in movement would be interesting, a key issue is whether viewers can accurately perceive sex in dynamic facial displays. Therefore, ratings from an objective sex-

identification task are a logical first step in investigating masculinity cues that lead to perceptual differences in stimuli. Correct identification of the sex of the male clips was 61%. This is not dissimilar to the values of 68% from Berry (1991) and about 60% from Hill and Johnston (2001), and reflects the difficulty of the task. This is not surprising given the apparent lack of anatomical constraints on facial movement; men and women can move their faces in any way they want, so it is interesting that facial movement was nevertheless diagnostic of sex.

There were some methodological considerations worth noting in our study. We used the forward counting method to estimate each woman's position in the menstrual cycle from the onset of last menstruation. This method is not as accurate as the reverse counting method because of the variability in the length of the follicular compared to the luteal phase. However, any inaccuracy will only have added noise to our data rather than systematic bias, and it is therefore noteworthy that we nevertheless found a robust effect with this relatively crude method. Furthermore, although the chance of conception may have predicted preferences for flirtatious facial movement, it is clearly not the mechanism underlying the preference shifts. After all, markedly different hormonal profiles can underlie the same mean conception probability. Recent studies examining preferences for masculinity in male faces have attempted to explicitly examine the endocrine correlates of preferences for artificially manipulated masculinity in faces (Welling et al., 2007) and preferences for male faces from men with measured testosterone (Roney & Simmons, 2008). These studies are somewhat contradictory, with the earlier study implicating women's testosterone levels in shifting preferences, while the latter suggests a key role for estradiol. Nevertheless, both studies suggest that cyclic shifts in hormone levels are closely associated with shifting preferences. Future research could search explicitly for associated hormonal fluctuations by measuring levels directly.

Determining what benefit women may actually gain by increasing their attraction to flirtatiousness during fertile peaks remains unresolved. Flirtatiousness may signal both direct benefits, via increased probability of reward for invested mating effort, and indirect benefits (i.e., good genes), via the costs involved in developing the necessary resources for producing skilled social behavior (cf. links between testosterone and mating display in other species). Menstrual cycle shifts in preferences are often described as favoring cues for indirect benefits, because conception is the only time when these benefits will actually be realized (although see Jones et al., 2005b for an alternative, although not necessarily incompatible exception, to this generalization). In this case, however, the direct benefits of conserving mating effort when faced with cues indicating that such effort will be wasted will also be of particular value to mid-cycle women, as the time

available during the fertile window is limited. Neither form of benefit can be excluded by our results, and it should be noted that they do not represent mutually exclusive alternatives; menstrual cycle shifts could serve both adaptive goals simultaneously (see Jones et al., 2008, for a related argument).

Studies of facial motion may be particularly important for menstrual cycle research, because the dynamics of a face can change quickly, unlike the static properties. For example, women can take advantage of a momentary opportunity when they see a man who is signaling interest by flirting. Improvements in motion capture technology mean that dynamic signals in the face can be investigated. Future investigations into cyclic changes in women's preferences may benefit from the consideration of such transient traits which may be important for potential exploitation of strategic mate choice opportunities.

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References

- Adkins-Regan, E. (2005). *Hormones and animal social behavior*. Princeton, NJ: Princeton University Press.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Bakker, T. C. M., Künzler, R., & Mazzi, D. (1999). Condition-related mate choice in sticklebacks. *Nature*, *401*, 234.
- Berry, D. S. (1991). Child and adult sensitivity to gender information in patterns of facial motion. *Ecological Psychology*, *3*, 349–366.
- Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Liu, C. K., Popovic, Z., et al. (2005). Dance reveals symmetry especially in young men. *Nature*, *438*, 1148–1150.
- Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low voice pitch among men. *Personality and Individual Differences*, *27*, 801–804.
- DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., et al. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society B*, *273*, 1355–1360.
- DeBruine, L. M., Jones, B. B., & Perrett, D. I. (2005). Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Hormones and Behavior*, *47*, 379–383.
- Feinberg, D. R., Jones, B. C., Law Smith, M. J. L., Moore, F. R., DeBruine, L. M., Cornwell, R. E., et al. (2006). Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Hormones and Behavior*, *49*, 215–222.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, *139*, 603–622.
- Fusani, L. (2008). Testosterone control of male courtship in birds. *Hormones and Behavior*, *54*, 227–233.
- 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. *Psychological Science*, *15*, 203–207.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society B*, *265*, 927–933.
- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society B*, *275*, 991–1000.
- Gralewski, L., Campbell, N., Morrison, E., & Penton-Voak, I. (2006). Analysis of facial dynamics using a tensor framework. *Journal of Multimedia*, *6*, 10–21.
- Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Hormones and Behavior*, *49*, 509–518.
- Haselton, M. G., Mortezaie, M., Pillsworth, E. G., Bleske-Rechek, A., & Frederick, D. A. (2007). Ovulatory shifts in human female ornamentation: Near ovulation, women dress to impress. *Hormones and Behavior*, *51*, 40–45.
- Heald, A. H., Ivison, F., Anderson, S. G., Cruickshank, K., Laing, I., & Gibson, J. M. (2003). Significant ethnic variation in total and free testosterone concentration. *Clinical Endocrinology*, *58*, 262–266.
- Hill, H., & Johnston, A. (2001). Categorizing sex and identity from the biological motion of faces. *Current Biology*, *11*, 880–885.
- Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of "quality" in women and men. *Evolution and Human Behavior*, *22*, 93–112.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone-mediated adaptive design. *Evolution and Human Behavior*, *22*, 251–267.
- Johnstone, R. A., Reynolds, J. D., & Deutsch, J. C. (1996). Mutual mate choice and sex differences in choosiness. *Evolution*, *50*, 1382–1391.
- Jones, B. C., DeBruine, L. M., Perrett, D. I., Little, A. C., Feinberg, D. R., & Law Smith, M. J. (2008). Effects of menstrual cycle phase on face preferences. *Archives of Sexual Behavior*, *37*, 78–84.
- Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Law Smith, M. J., et al. (2005a). 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. *Hormones and Behavior*, *48*, 283–290.
- Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. E., et al. (2005b). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society B*, *272*, 347–354.
- Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits, and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality*, *58*, 97–116.
- Lander, K. (2008). Relating vocal and visual attractiveness for moving and static faces. *Animal Behaviour*, *75*, 817–822.
- Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*, 390–423.
- Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Preferences for symmetry in faces change across the menstrual cycle. *Biological Psychology*, *76*, 209–216.
- Maynard Smith, J. (1956). Fertility, mating behaviour and sexual selection in *Drosophila subobscura*. *Journal of Genetics*, *54*, 261–279.
- Mishra, S., Clark, A. P., & Daly, M. (2007). One woman's behavior affects the attractiveness of others. *Evolution and Human Behavior*, *28*, 145–149.
- Møller, A. P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: A meta-analysis. *American Naturalist*, *151*, 174–192.
- Morrison, E. R., Gralewski, L., Campbell, N., & Penton-Voak, I. S. (2007). Facial movement varies by sex and is related to attractiveness. *Evolution and Human Behavior*, *28*, 186–192.
- Pawłowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology*, *70*, 38–43.
- Penton-Voak, I. S., & Chang, H. (2008). Attractiveness judgments of individuals vary across emotional expression and movement conditions. *Journal of Cultural and Evolutionary Psychology*, *6*, 89–100.

- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, 25, 229–241.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39–48.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741–742.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, 394, 884–887.
- Pound, N., Penton-Voak, I. S., & SurrIDGE, A. K. (2009). Testosterone responses to competition in men are related to facial masculinity. *Proceedings of the Royal Society B*, 276, 153–159.
- Provost, M. P., Quinsey, V. L., & Troje, N. F. (2008a). Differences in gait across the menstrual cycle and their attractiveness to men. *Archives of Sexual Behavior*, 37, 598–604.
- Provost, M. P., Troje, N. F., & Quinsey, V. L. (2008b). Short-term mating strategies and attraction to masculinity in point-light walkers. *Evolution and Human Behavior*, 29, 65–69.
- Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Jones, B. C., Carter, V., et al. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, 26, 213–226.
- Roney, J. R., Hanson, K. N., Durante, K. M., & Maestripieri, D. (2006). Reading men's faces: Women's mate attractiveness judgments track men's testosterone and interest in infants. *Proceedings of the Royal Society B*, 273, 2169–2175.
- Roney, J. R., & Simmons, Z. L. (2008). Women's estradiol predicts preference for facial cues of men's testosterone. *Hormones and Behavior*, 53, 14–19.
- Rowland, W. J. (1995). Do female sticklebacks care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour*, 132, 951–961.
- Rubenstein, A. J. (2005). Variation in perceived attractiveness. *Psychological Science*, 16, 759–762.
- Scarborough, P. S., & Johnston, V. S. (2005). Individual differences in women's facial preferences as a function of digit ratio and mental rotation ability. *Evolution and Human Behavior*, 26, 509–526.
- Simpson, J. A., Gangestad, S. W., & Biek, M. (1993). Personality and nonverbal social behaviour: An ethological perspective of relationship initiation. *Journal of Experimental Social Psychology*, 29, 434–461.
- Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., et al. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones and Behavior*, 52, 156–161.
- Wilcox, A. J., Dunson, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of conception with a single act of intercourse: Providing benchmark rates for assessment of post-coital contraceptives. *Contraception*, 63, 211–215.
- Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to “bad genes” and the anomalous face overgeneralization effect: Cue validity, cue utilization, and accuracy in judging intelligence and health. *Journal of Nonverbal Behavior*, 28, 167–185.