



Do women's faces become more attractive near ovulation?

Tikal M. Catena^a, Zachary L. Simmons^{a,b}, James R. Roney^{a,*}

^a University of California, Santa Barbara, United States of America

^b University of Portland, United States of America

ARTICLE INFO

Keywords:

Menstrual cycle
Attractiveness
Estradiol
Progesterone

ABSTRACT

There have been mixed findings regarding whether raters judge women's natural faces more attractive when the women were photographed near ovulation relative to when photographed in other cycle regions. Bobst and Lobmaier (2012) isolated shape cues associated with ovulatory timing via computer morphing techniques and found that men judged face shapes characteristic of the fertile window as more attractive than those characteristic of the luteal phase. Here, we tested replication of their findings but also added stimuli from the early follicular phase. We constructed three composite faces constructed from photos of the same 23 women who had each been photographed in the early follicular phase, during the fertile window, and during the luteal phase. We next warped 20 other identity faces to the shapes of the composite faces representing each cycle phase, and asked male participants to rank order the resulting face triplets for attractiveness. Men ranked fertile window and luteal phase stimuli as more attractive than early follicular stimuli, but ranked fertile window and luteal phase faces as equally attractive. This result failed to replicate preferences for fertile window over luteal phase stimuli, and thereby argues against perceivers' ability to detect face shape cues of immediate fecundity. Because estradiol was lower in the early follicular phase relative to the other two cycle phases, our findings are consistent with the possibility that within-women increases in estradiol produce subtle increases in face shape attractiveness. Discussion addresses the overall evidence for facial cues of women's ovulatory timing.

1. Introduction

Are there subtle changes in women's facial appearance that act as cues of ovulatory timing? Females in many nonhuman mammals, including many primate species, produce clear signals of current fecundity (for reviews, see Dixon, 1998; Thornhill and Gangestad, 2008). Human ovulatory timing is not overtly signaled, but various studies have argued for detectable changes in women's voices, faces, odors, and behaviors that may be associated with within-cycle shifts in fecundity (for reviews, see Haselton and Gildersleeve, 2011, 2016). The present research will specifically address possible shifts in women's facial appearance.

Research on cycle phase shifts in the attractiveness of natural faces has been mixed. Roberts et al. (2004) argued that raters were slightly more likely to judge photos of women taken during the late follicular phase as more attractive than photos of the same women taken during the luteal phase. Effects were only significant for subsets of raters and stimulus presentation techniques, however, and cycle phase estimation relied on counting methods that have substantial measurement error (see Gangestad et al., 2016). In addition, Bleske-Rechek et al. (2011) failed to replicate these results using similar methods.

Other studies have assessed hormonal correlates of within-women changes in natural face attractiveness. Puts et al. (2013) photographed women twice, once during the estimated ovulatory phase and once in the estimated luteal phase, and collected attractiveness ratings of the natural faces. Changes in progesterone across the two days negatively predicted changes in face attractiveness, with null effects for changes in estradiol (both in isolation and in interaction with progesterone). Because estradiol often does not differ between late follicular and luteal samples (see below), however, this study may not have been able to test effects of estradiol on face attractiveness; in addition, the study did not directly estimate cycle phase effects. Finally, Jones et al. (2018) photographed a large sample of 249 women at five weekly intervals with salivary hormone measures collected on corresponding days and found only a negative interaction between estradiol and progesterone ($p = .03$) in predicting within-women shifts in ratings of face attractiveness. This study did not estimate position in the cycle, and analyses showed that attractiveness ratings were highest when estradiol was high and progesterone low but also when progesterone was high and estradiol low, which the authors argued is not fully consistent with greater attractiveness near ovulation. Thus, studies that have measured within-women changes in both hormones and natural face

* Corresponding author at: Department of Psychological and Brain Sciences, University of California, Santa Barbara, CA 93106-9660, United States of America.
E-mail address: roney@psych.ucsb.edu (J.R. Roney).

<https://doi.org/10.1016/j.yhbeh.2019.07.008>

Received 22 March 2019; Received in revised form 8 July 2019; Accepted 12 July 2019

Available online 26 July 2019

0018-506X/ © 2019 Elsevier Inc. All rights reserved.

attractiveness have produced ambiguous evidence that attractiveness increases near ovulation.

Bobst and Lobmaier (2012) took a different approach to this issue by isolating face shapes characteristic of different cycle phases. A sample of 25 women were photographed in both the late follicular phase (confirmed by scheduling photographs within 24 h. of positive luteinizing hormone (LH) tests) and seven days later in the luteal phase. The 25 photos from each phase were morphed together to form average facial composites associated with each cycle phase. Twenty new faces were then each stretched to the shapes associated with the ovulatory and luteal composite faces, and raters judged which of the two versions of each of the 20 faces was more attractive. The authors reported that men judged the follicular phase faces as more attractive at rates significantly above chance. They also suggested that the face shape changes may have been due to changes in progesterone, since for the 25 women who were photographed twice, salivary progesterone was higher in the luteal sessions but salivary estradiol did not differ across the two time points.

The **Bobst and Lobmaier (2012)** paper provides evidence that women's face shape may change in subtle ways near ovulation relative to the luteal phase. Because the 20 identity faces maintained their original color and texture when stretched to the shapes of the ovulatory and luteal prototypes, only shape information was manipulated by the authors' technique. The morphing technique for construction of the face prototypes should isolate those cues that vary with cycle position, which may have allowed the detection of shape changes that might be too subtle to detect when rating natural faces one at a time. The use of LH tests to estimate cycle phase position was also an improvement on past studies in this area, providing greater confidence regarding cycle region.

Our general goal here is to test replication of the **Bobst and Lobmaier (2012)** findings in an independent sample of faces. Independent replication may be especially important given that other studies have used versions of the original **Bobst and Lobmaier (2012)** stimuli to test claims about responses to facial cues of ovulatory timing. **Krems et al. (2016)**, for example, used the face prototypes from **Bobst and Lobmaier (2012)** to test women's mate guarding responses to cues of ovulatory timing. In addition, a subset of the original 25 faces used to make the cycle phase prototypes were used to make new (but highly similar and non-independent) prototypes that were used to test women's responses to ovulatory cues (**Lobmaier et al., 2016**) and the relationship between men's testosterone and their reaction to such cues (**Bobst and Lobmaier, 2014**). Since the stimuli in all of these studies were derived from the same pool of faces, what appear to be multiple demonstrations of responses to ovulatory cues are actually non-independent effects, highlighting the need for independent replication.

Furthermore, the prototypes in **Bobst and Lobmaier (2012)** compared only the late follicular to the luteal phase. Although this approach is common in cycle phase research, it leaves unknown whether face shapes characteristic of the ovulatory region are considered more attractive than shapes characteristic of all other cycle regions, including the early follicular phase. This issue is relevant to how precise cues of ovulatory timing may be, as it is possible that the effects in **Bobst and Lobmaier (2012)** were due to drops in attractiveness that are specific to the luteal phase rather than to elevations in attractiveness that are more precisely associated with days when conception is possible. This also relates to the question of hormonal correlates of changes in face shape, since **Bobst and Lobmaier (2012)** constructed face prototypes from cycle days that did not differ in estradiol concentrations.

In the present study, we used an independent set of face photographs to test replication of the effects reported in **Bobst and Lobmaier (2012)**. In addition, because we had a sample of women who were photographed repeatedly across the cycle, we were able to construct face shape prototypes from the follicular phase before the ovulatory region, in addition to prototypes constructed near ovulation and during the luteal phase. This distribution also allowed us to isolate the

potential influence of both estradiol and progesterone on ratings of facial attractiveness: mean estradiol concentrations were lower in the early follicular phase than in the ovulatory and luteal phases, whereas progesterone concentrations were higher in the luteal phase relative to the other two cycle regions.

2. Methods

2.1. Participants

One hundred twenty-three English speaking male participants were recruited through Amazon MTurk and paid US \$2 for completing the study (average participation time was 6.1 min). Six participants who reported a homosexual orientation were excluded from data analyses. Three subjects who exceeded a time constraint of 15 min for completion of the survey were excluded due to the likelihood that this represented a discontinuous engagement in the study. Finally, another two subjects were excluded for submitting a high percentage of invalid ranking responses (e.g., ranking two faces as 'Least Attractive'). Of the remaining men, aged 19–54 (mean = 27.79 ± 5.7 years), 61 reported being in a relationship, while 51 reported being single.

2.2. Face stimuli

2.2.1. Face selection across cycle phases

Women participants whose face photographs were used to construct cycle phase prototypes were part of a broader study that examined hormonal correlates of mating psychology and behavior (**Roney and Simmons, 2013, 2016**). A total of 52 women took part in this study. Exclusion criteria included pregnancy, lactation, or any use of hormonal contraceptives within the last six months, as well as self-reported menstrual cycles longer than 40 days. In addition to completing daily diary measures, women attended four weekly laboratory sessions across 1–2 menstrual cycles during which we took face and full body photos with a digital camera at a standard distance. (The full body photos were used in prior publications that tested hormonal correlates of women's body attractiveness, as well as cycle phase shifts in their clothing choices; see **Eisenbruch et al., 2015; Grillot et al., 2014**.) Make-up use was not controlled, but should not have affected the face stimuli presented to participants in the present study since our warping procedure retained the original color and texture of the natural faces that were stretched to the shapes of cycle phase composites (see [section 2.2.2](#) below). Women were asked to adopt a neutral expression for the face photographs.

Saliva samples were collected from the women via passive drool during each laboratory session. In addition, women collected daily saliva samples each morning as part of the broader study. We sent for assay all of the daily samples in a nine-day window surrounding the estimated day of ovulation (computed as 15 days before the end of each cycle), as well as samples from alternating days outside of this window. All of the laboratory session samples were sent for assay. Samples were assayed in duplicate for estradiol, progesterone, and testosterone at the Endocrine Core Laboratory at the California Regional Primate Research Center in Davis, CA. Progesterone was assayed using commercial radioimmunoassay kits modified to accommodate salivary sampling. Testosterone was assayed in duplicate using double-antibody commercial radioimmunoassay kits. Estradiol was assayed using high sensitivity immunoassay kits from Salimetrics. Full details of the assay procedures appear in **Roney and Simmons (2013)** and **Eisenbruch et al. (2015)**; intra- and inter-assay CVs were below 10% for each hormone.

The daily hormone values were used to estimate cycle phase for each of the laboratory sessions in which photos were taken. Following **Ellison et al. (1987)**, we judged a cycle as ovulatory if its maximum progesterone value exceeded 300 pmol/l. For the ovulatory cycles, we followed **Lipson and Ellison (1996)** in using the mid-cycle estradiol drop to estimate the day of ovulation: we identified the day of peak

estradiol (conditional on this day preceding the luteal phase rise in progesterone), and then estimated the day of ovulation as the day after this peak with the largest drop in estradiol from the previous day (see also Roney and Simmons, 2017). The fertile window (i.e. cycle days on which conception is possible) was then defined as the day of ovulation and the preceding five days (Wilcox et al., 1998).

Once we had estimates of the day of ovulation in the ovulatory cycles, we could estimate three cycle regions for selection of face photographs: the follicular phase before the fertile window (earlier than day -5 relative to ovulation as day zero), during the fertile window (days -5 to 0), and the luteal phase after the fertile window (all days greater than zero). Out of the original 52 women who took part in the study, daily saliva samples were sent for assay for 43 of them (those with many missing samples were not sent for assay); among these 43 women, 34 were judged to have had at least one ovulatory cycle. Since many women participated across two menstrual cycles, we had a set of 52 ovulatory cycles that included face photographs.

We next searched for women who had face photographs across all three of our targeted cycle phases. Twenty-three such cases were identified (mean age = 19.04 ± 0.30 years). All follicular phase photos selected for use were taken between days -11 and -6 (mean = -8.87 ± 0.35), fertile window photos between days -5 and 0 (mean = -2.13 ± 0.32), and luteal phase photos between days $+4$ and $+9$ (mean = 7.17 ± 0.32).

2.2.2. Stimulus construction

Face stimuli were constructed in two steps. Using the Webmorph facial manipulation software (DeBruine, 2017), the 23 facial photographs from each phase were morphed together by averaging the location of 189 landmark points that marked consistent facial structures. By including the same set of women in each morph, this procedure should isolate those cues that vary across the respective cycle phases, thus creating representative prototypes. The three composite faces are depicted in Fig. 1.

Next, following Bobst and Lobmaier (2012), we selected 20 women's face photos with neutral expressions from the Karolinska Directed Emotional Faces (KDEF) database and stretched ("warped") them toward the shapes of the three cycle phase composites using the same landmark points. The Webmorph program transformed the natural faces based solely on shape, moving landmark points on those faces toward their location on the composite face targets while retaining the original color and texture of the Karolinska sample faces; as such, any effects of make-up use on the faces used to construct the cycle phase composites should not be present in the final stimuli. Following Bobst and Lobmaier (2012), two warps were created for each pairing of natural face and cycle phase morph, varying only in their degree of

transformation: 50% warps moved landmark points on the natural faces half the distance toward their position on the morphed faces, whereas 100% warps moved them the full distance. This resulted in 120 total faces (20 faces \times 3 cycle phases \times 2° of transformation). Fig. 2 presents an example of one natural face that has been stretched to the shapes of the three cycle phase morphs across both degrees of transformation. Our methods for stimulus creation were identical to those used by Bobst and Lobmaier (2012), save for the inclusion of an early follicular phase prototype and the use of different software. However, our software (Webmorph) is a web-based version of the software employed by Bobst and Lobmaier (Psychomorph), so differences in performance should be minimal.

2.2.3. Hormone differences across cycle phase

The face morphs in Fig. 1 may isolate changes in face shape that are related to cycle phase associated changes in ovarian hormones. We used the hormone values assayed from saliva samples collected during the photo sessions to test whether hormone concentrations differed within-women across the three sampled cycle regions. Repeated measures ANOVA showed differences across phases in estradiol, $F(2, 44) = 3.28$, $p < .05$, $\eta_p^2 = 0.13$ and progesterone, $F(2, 38) = 61.17$, $p < .00001$, $\eta_p^2 = 0.76$, but not in testosterone, $F(2, 44) = 0.02$, $p = .98$, $\eta_p^2 = 0.001$. Fig. 3 depicts the relevant data for estradiol and progesterone. Pairwise contrasts revealed that estradiol was lower in the pre-fertile window follicular phase relative to both the fertile window ($ps < 0.01$, $d = 0.60$) and the luteal phase ($p < .05$, $d = 0.44$), whereas the fertile window and luteal phases did not differ ($p = .98$, $d = 0.00$). For progesterone, such contrasts showed much higher values in the luteal phase relative to both the pre-fertile window follicular phase ($p < .001$, $d = 1.62$) and the fertile window ($p < .001$, $d = 1.63$), whereas progesterone did not differ between the pre-fertile window and the fertile window ($p = .20$, $d = 0.31$). Thus, the luteal phase morph isolates a cycle region when progesterone was uniquely high relative to the other two regions, whereas the pre-fertile window follicular phase morph isolates a region that was uniquely low in estradiol.

2.3. Ranking procedure

Rankings were collected through the Qualtrics online surveying software. Following an attention check, raters were randomly assigned to either the 50% or 100% transformation condition. Next, they were presented with each of the 20 triplets within their condition, with each triplet's three faces displayed simultaneously, and asked to rank them by facial attractiveness from 1 (Most attractive) to 3 (Least attractive) using a drop-down list. The order in which the triplets were presented



Fig. 1. Follicular phase, fertile window, and luteal phase face prototypes (from left to right). Each face is a morphed composite constructed from photos of the same 23 women that were taken during the respective cycle phases.

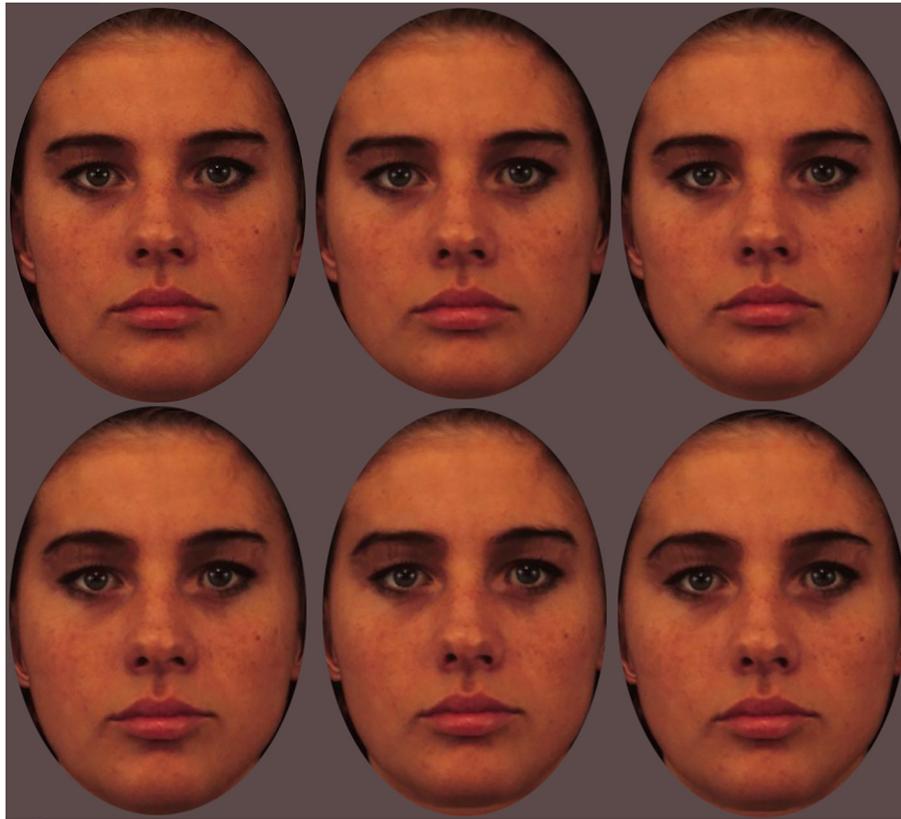


Fig. 2. Sample stimuli. Individual stimulus triplets in which a face was transformed 50% (top panel) and 100% (bottom panel) toward the respective follicular phase, fertile window, and luteal phase prototypes (from left to right).

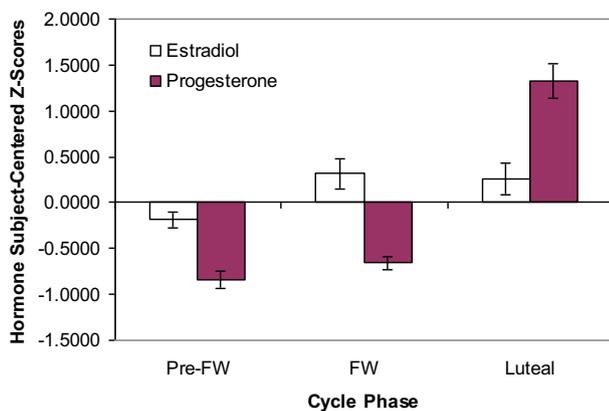


Fig. 3. Mean estradiol and progesterone concentrations associated with the photo sessions that occurred during each of the three indicated cycle phases. Hormone values were first grand-mean standardized but then centered within women, such that zero on the y-axis represents a woman's mean hormone concentration across all of her photo sessions. Error bars are \pm s.e.m. FW = fertile window.

was randomized, as was the position of faces within each triplet. Following this, anonymous demographic information was collected, including age, sexual orientation, and relationship status. These procedures were approved by the local Institutional Review Board.

There were 99 cases for which participants submitted invalid rankings (e.g., ranking two faces as 'Least Attractive'). These represented 1.9% of total responses. These cases were excluded from the Results presented below, though no statistical conclusions would be changed via their inclusion.

3. Results

As a first pass at the data analyses, we computed a mean ranking for each male participant for each type of face warp (pre-fertile window, fertile window, luteal) across the 20 face triplets. We then used repeated measures ANOVA to test whether mean rankings differed across the stimulus types, with pairwise contrasts between individual cycle phases as follow-ups to significant main effects. Partial eta-squared and Cohen's d are reported as effect size measures for ANOVA main effects and pairwise contrasts, respectively.

For the 50% warps, there was no difference in mean rankings, $F(2, 106) = 0.31$, $p = .74$, $\eta_p^2 = 0.01$. For the 100% warps, mean rankings did differ across stimulus types, $F(2, 114) = 13.50$, $p < .001$, $\eta_p^2 = 0.19$. Mean rankings were 2.13 ± 0.03 for the follicular phase stimuli, 1.93 ± 0.02 for the fertile window stimuli, and 1.94 ± 0.03 for the luteal stimuli. Pairwise contrasts in the repeated measures ANOVA revealed that the pre-fertile window follicular phase stimuli were ranked higher (i.e. less attractive) than both the fertile window ($p < .001$, $d = 0.60$) and luteal stimuli ($p < .01$, $d = 0.47$), but the fertile window and luteal stimuli rankings did not differ ($p = .63$, $d = 0.04$). Fig. 4 presents the percent of times each stimulus type was ranked first, second, or third, aggregated across the 100% warp trials. Although the ranking pattern for the pre-fertile window follicular stimuli differed from that for the other two phases, there was also clearly substantial overlap in the tendency for each stimulus type to receive each of the three possible ranks.

As a check on the robustness of the repeated measures ANOVA results, we re-analyzed the data using multi-level, multinomial (ordinal) logistic regression models computed in SPSS v24. For these models, face triplets were nested within male participants, and the models used all of the available data instead of relying on mean rankings for each male participant. Effects of stimulus type were allowed to vary randomly

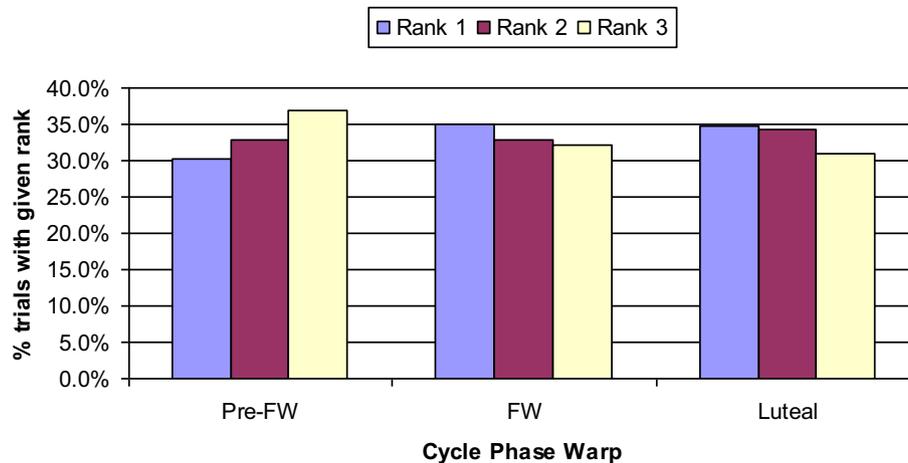


Fig. 4. Percentage of times that each cycle phase stimulus was ranked first, second, or third, aggregated across the 100% transformation trials. FW = fertile window.

across subjects. For the 50% warps, there were no significant differences in within-subject rankings ($p > 0.35$). For the 100% morphs, there was an overall effect of stimulus type ($p < .001$), pre-fertile window stimuli were ranked higher (i.e. less attractive) than stimuli from each of the other two phases ($p < 0.001$), and rankings did not differ between the fertile window and luteal phase stimuli ($p = .70$). Thus, ordinal regression analysis produced essentially the same results as repeated measures ANOVA.

4. Discussion

Bobst and Lobmaier (2012) provided perhaps the most direct evidence that women's face shape may become more attractive near ovulation relative to other times in the menstrual cycle. Here, we used their same methods but with an independent face set and the addition of target faces drawn from the pre-fertile window follicular phase. Our results mostly failed to replicate their findings. For the 50% morphs—for which ovulatory stimuli were judged more attractive than luteal stimuli in Bobst and Lobmaier (2012)—there were no differences in rankings of attractiveness across stimuli created from three cycle phase regions. For the 100% morphs, early follicular face stimuli were ranked as less attractive than fertile window and luteal stimuli, which were ranked equally attractive. This result fails to replicate greater face attractiveness during the fertile window relative to the luteal phase.

Our findings raise doubts about whether there are face shape cues of women's fecundity. Although fertile window stimuli were ranked more attractive than stimuli from earlier in the follicular phase, the fact that luteal phase stimuli were just as attractive as those from the fertile window suggests that observers did not consistently prefer stimuli associated with higher fecundity. In addition, despite statistically significant results, there were high amounts of overlap in ranking patterns for the three types of stimuli (Fig. 4).

The addition of stimuli created from faces photographed in the early follicular phase allowed us to isolate cycle regions that differed in both estradiol and progesterone, whereas Bobst and Lobmaier (2012) compared regions that differed only in progesterone. Our findings were most consistent with a positive effect of estradiol on face attractiveness. Estradiol was lowest in the pre-fertile window follicular phase but equal in the other two phases (Fig. 3), and this corresponded to face stimuli having been ranked least attractive in the early follicular phase but equal in the other two cycle regions. If progesterone had a negative effect on face attractiveness, luteal phase stimuli should have been ranked less attractive than fertile window stimuli. Alternatively, simultaneous positive effects of estradiol and negative effects of progesterone should have produced heightened face attractiveness for the fertile window stimuli relative to each of the other two phases. Because

prior comparisons of peri-ovulatory and luteal stimuli (Bobst and Lobmaier, 2012; Puts et al., 2013) compared cycle regions that do not generally differ in estradiol concentrations, they were likely not capable of detecting effects of estradiol. Jones et al. (2018), however, did assess shifts in face attractiveness across broader cycle regions and found no significant correlations with within-women fluctuations in estradiol concentrations, albeit in natural faces, which is contrary to the patterns reported here.

A positive effect of estradiol on face shape attractiveness, if reliable, would not directly support the common proposal that women are signaling or leaking cues of within-cycle fecundity. Estradiol is much higher in ovulatory than in anovulatory menstrual cycles, and is also elevated across cycle regions in cycles with higher conception probabilities (Lipson and Ellison, 1996; Venner's et al., 2006). Thus, subtle changes in face attractiveness associated with higher estradiol may act as cues that women are experiencing ovulatory cycles, rather than acting as cues of fertile window timing. This conjecture is consistent with our finding of higher face attractiveness in both the fertile window and luteal phase when estradiol was elevated, relative to the early follicular phase when concentrations of ovarian hormones were low. The literature on cues of ovulatory timing in humans has generally neglected the possibility that subtle changes in women's attractiveness are byproducts of cues associated with shifts in fecundity across longer time-scales than individual cycles, despite the fact that many findings are consistent with this possibility (see Roney, 2009). It remains possible in principle that with frequent exposure to the same woman over many cycles, an observer might be able to more reliably detect subtle visual cues of fertile window timing, though empirical research is necessary to test that conjecture.

Our current findings in conjunction with mixed findings for effects of cycle phase on natural face attractiveness (Roberts et al., 2004; Bleske-Rechek et al., 2011; see Introduction) suggest that there is insufficient evidence to conclude that women's faces become more attractive near ovulation. Studies that have measured hormonal correlates of within-women shifts in natural face attractiveness have also produced mixed results, as a negative association between changes in progesterone and shifts in face attractiveness across two time points (Puts et al., 2013) was not replicated in a larger study with five weekly measurements (Jones et al., 2018), which instead found only an interaction between estradiol and progesterone that the authors argued was not consistent with fertile window increases in attractiveness. Thus, we believe that the null hypothesis of no ovulatory shifts in face attractiveness should not be rejected based on current evidence.

The question of whether humans can detect cues of ovulatory timing is theoretically significant given that most major theories of the evolution of human pair bonding posit concealment of current fecundity as

necessary for the emergence of male long-term investment in mates and offspring (e.g., Alexander, 1990; Sillén-Tullberg and Moller, 1993; Strassmann, 1981). Our current findings failed to support the clear detection of such cues in women's faces, but do not speak to potential ovulatory shifts in the perceived attractiveness of women's odors, bodies, voices, and behaviors (for a review of evidence for such shifts, see Haselton and Gildersleeve, 2011, 2016). An important empirical and conceptual issue for this area of investigation is an assessment of whether any such cues of ovulatory timing are diagnostic enough that they challenge the assumptions of concealed ovulation posited by theories that seek to explain the evolution of human pair bonding.

Acknowledgments

This research was supported by a Hellman Family Faculty Fellowship and UCSB Academic Senate Grant to J.R.R., and by a UCSB URCA Grant to T.M.K. Funding sources had no role in data collection, analysis, writing, or the decision to publish.

References

- Alexander, R.D., 1990. How did humans evolve. *Museum Zool* 1, 1–38 Univ. Michigan Spec. Publ.
- Bleske-Rechek, A., Harris, H.D., Denking, K., Webb, R.M., Erickson, L., Nelson, L.A., 2011. Physical cues of ovulatory status: a failure to replicate enhanced facial attractiveness and reduced waist-to-hip ratio at high fertility. *Evol. Psychol.* 9 (3), 336–353 (<https://doi.org/epjournal-1461> [pii]).
- Bobst, C., Lobmaier, J.S., 2012. Men's preference for the ovulating female is triggered by subtle face shape differences. *Horm. Behav.* 62 (4), 413–417. <https://doi.org/10.1016/j.yhbeh.2012.07.008>.
- Bobst, C., Lobmaier, J.S., 2014. Is preference for ovulatory female's faces associated with men's testosterone levels? *Horm. Behav.* 66 (3), 487–492. <https://doi.org/10.1016/j.yhbeh.2014.06.015>.
- DeBruine, L., 2017. Webmorph (Version v0.0.0.9001). Zenodo <https://doi.org/10.5281/zenodo.1073696>.
- Dixson, A.F., 1998. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Humans*. Oxford University Press, Oxford.
- Eisenbruch, A.B., Simmons, Z.L., Roney, J.R., 2015. Lady in red: hormonal predictors of women's clothing choices. *Psychol. Sci.* 26 (8), 1332–1338. <https://doi.org/10.1177/0956797615586403>.
- Ellison, P.T., Lager, C., Calfee, J., 1987. Low profiles of salivary progesterone among college undergraduate women. *J. Adolesc. Health Care* 8 (2), 204–207. [https://doi.org/10.1016/0197-0070\(87\)90266-X](https://doi.org/10.1016/0197-0070(87)90266-X).
- Gangestad, S.W., Haselton, M.G., Welling, L.L.M., Gildersleeve, K., Pillsworth, E.G., Burriss, R.P., Larson, C.M., Puts, D.A., 2016. How valid are assessments of conception probability in ovulatory cycle research? Evaluations, recommendations, and theoretical implications. *Evol. Hum. Behav.* 37 (2), 85–96. <https://doi.org/10.1016/j.evolhumbehav.2015.09.001>.
- Grillot, R.L., Simmons, Z.L., Lukaszewski, A.W., Roney, J.R., 2014. Hormonal and morphological predictors of women's body attractiveness. *Evol. Hum. Behav.* 35 (3), 176–183. <https://doi.org/10.1016/j.evolhumbehav.2014.01.001>.
- Haselton, M.G., Gildersleeve, K., 2011. Can men detect ovulation? *Curr. Dir. Psychol. Sci.* 20 (2), 87–92. <https://doi.org/10.1177/0963721411402668>.
- Haselton, M.G., Gildersleeve, K., 2016. Human ovulation cues. *Curr. Opin. Psychol.* 7, 120–125.
- Jones, B.C., Hahn, A.C., Fisher, C.I., Wang, H., Kandrik, M., Lao, J., Han, C., Lee, A.J., Holzleitner, I.J., DeBruine, L.M., 2018. No compelling evidence that more physically attractive young adult women have higher estradiol or progesterone. *Psychoneuroendocrinology* 98, 1–5. <https://doi.org/10.1016/j.psyneuen.2018.07.026>.
- Krems, J.A., Neel, R., Neuberg, S.L., Puts, D.A., Kenrick, D.T., 2016. Women selectively guard their (desirable) mates from ovulating women. *J. Pers. Soc. Psychol.* 110 (4), 551–573. <https://doi.org/10.1037/pspi0000044>.
- Lipson, S.F., Ellison, P.T., 1996. Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum. Reprod.* 11 (10), 2090–2096. <https://doi.org/10.1093/oxfordjournals.humrep.a019055>.
- Lobmaier, J.S., Bobst, C., Probst, F., 2016. Can women detect cues to ovulation in other women's faces? *Biol. Lett.* 12, 20150638. <https://doi.org/10.1098/rsbl.2015.0638>.
- Puts, D.A., Bailey, D.H., Cárdenas, R.A., Burriss, R.P., Welling, L.L.M., Wheatley, J.R., Dawood, K., 2013. Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Horm. Behav.* 63 (1), 13–19. <https://doi.org/10.1016/j.yhbeh.2012.11.007>.
- Roberts, S.C., Havlicek, J., Flegr, J., Hruskova, M., Little, A.C., Jones, B.C., Perrett, D.I., Petrie, M., 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proc. R. Soc. London B* 271, S270–S272. <https://doi.org/10.1098/rsbl.2004.0174>.
- Roney, J.R., 2009. The role of sex hormones in the initiation of human mating relationships. In: Ellison, P.T., Gray, P.B. (Eds.), *The Endocrinology of Social Relationships*. Harvard University Press, Cambridge, MA, pp. 246–269.
- Roney, J.R., Simmons, Z.L., 2013. Hormonal predictors of sexual motivation in natural menstrual cycles. *Horm. Behav.* 63 (4), 636–645. <https://doi.org/10.1016/j.yhbeh.2013.02.013>.
- Roney, J.R., Simmons, Z.L., 2016. Within-cycle fluctuations in progesterone negatively predict changes in both in-pair and extra-pair desire among partnered women. *Horm. Behav.* 81, 45–52. <https://doi.org/10.1016/j.yhbeh.2016.03.008>.
- Roney, J.R., Simmons, Z.L., 2017. Ovarian hormone fluctuations predict within-cycle shifts in women's food intake. *Horm. Behav.* 90, 8–14. <https://doi.org/10.1016/j.yhbeh.2017.01.009>.
- Sillén-Tullberg, B., Moller, A.P., 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *Am. Nat.* 141 (1), 1–25.
- Strassmann, B.I., 1981. Sexual selection, paternal care, and concealed ovulation in humans. *Ethol. Sociobiol.* 2 (1), 31–40. [https://doi.org/10.1016/0162-3095\(81\)90020-0](https://doi.org/10.1016/0162-3095(81)90020-0).
- Thornhill, R., Gangestad, S.W., 2008. *The Evolutionary Biology of Human Female Sexuality*. Oxford University Press, Oxford.
- Venners, S.A., Liu, X., Perry, M.J., Korricks, S.A., Li, Z., Yang, F., Yang, J., Lasley, B.L., Xu, X., Wang, X., 2006. Urinary estrogen and progesterone metabolite concentrations in menstrual cycles of fertile women with non-conception, early pregnancy loss or clinical pregnancy. *Hum. Reprod.* 21 (9), 2272–2280. <https://doi.org/10.1093/humrep/del187>.
- Wilcox, A.J., Weinberg, C.R., Baird, D.D., 1998. Post-ovulatory ageing of the human oocyte and embryo failure. *Hum. Reprod.* 13 (2), 394–397. <https://doi.org/10.1093/humrep/13.2.394>.