Evolution and Human Behavior 35 (2014) 9–16

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Hormones and social monitoring: Menstrual cycle shifts in progesterone underlie women's sensitivity to social information ☆

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ARTICLE INFO

Article history:
Initial receipt 24 January 2013
Final revision received 1 September 2013

Keywords:
Progesterone
Hormones
Social cognition
Attention
Categorization
Menstrual cycle

ABSTRACT

During the luteal phase of the menstrual cycle, women's bodies prepare themselves for possible pregnancy and this preparation includes a dramatic increase in progesterone. This increase in progesterone may underlie a variety of functionally relevant psychological changes designed to help women overcome challenges historically encountered during pregnancy (e.g., warding off social threats and recruiting allies). This paper reports data supporting the hypothesis that increases in progesterone during the luteal phase underlie heightened levels of social monitoring—that is, heightened sensitivity to social cues indicating the presence of social opportunity or threat. Increases in progesterone during the luteal phase were associated with increased accuracy in decoding facial expressions (Study 1) and increased attention to social stimuli (Study 2). Findings suggest that increases in progesterone during the luteal phase may be linked functionally with low-level perceptual attunements that help women effectively navigate their social world.

To navigate the challenges of everyday social life, people must be keenly aware of the opportunities and threats afforded by other people. Indeed, people are profoundly sensitive to information indicating the presence of others who might help or harm them (Ackerman et al., 2009; Delton et al., 2012; DeWall, Maner, & Rouby, 2009; Öhman & Mineka, 2001). Although an emerging literature has revealed a number of factors that affect people's sensitivity to social information, less is known about how this sensitivity is guided by evolved physiological processes. In this paper we use an adaptationist framework to investigate a relatively covert yet powerful physiological determinant of women's sensitivity to social information. In two studies, we test the hypothesis that increases in progesterone during the luteal phase of the menstrual cycle promote heightened sensitivity to social cues.

1. Luteal phase increases in progesterone prepare the body for pregnancy

The luteal phase of a woman's menstrual cycle (the period immediately following ovulation and lasting until the onset of menstruation) is marked by her body's preparation for possible pregnancy. During this time, the dominant follicle turns into the corpus luteum, the endometrium thickens, and body temperature increases—all to promote the growth of a fertilized egg (Gilbert, 2000). Notably, these changes occur regardless of whether conception has actually occurred. This is consistent with the logic of error management theory (Haselton & Buss, 2000; Haselton & Nettle, 2006): the energetic costs of preparing for possible pregnancy in the absence of conception are outweighed by the reproductive costs of failing to generate the necessary environment for the growth of a fertilized egg. Thus, during the luteal phase of each menstrual cycle, a woman's body prepares itself for possible pregnancy whether or not an egg has actually been fertilized.

From an adaptationist perspective, the physiological changes initiated during the luteal phase should underlie relevant psychological processes designed to overcome challenges historically associated with pregnancy (Conway et al., 2007; Fessler, 2002; Jones et al., 2005; Navarrete, Fessler, & Eng, 2007). For example, to prevent their bodies from rejecting a growing fetus, women experience suppressed immune system functioning during the luteal phase, and this immunosuppression increases their vulnerability to forms of contagious illness (Robinson & Klein, 2012). Consequently, immunosuppression during the luteal phase is accompanied by corresponding psychological processes aimed at helping women avoid potential disease: During the luteal phase (and into the first trimester of pregnancy), women display high sensitivity to disgusting stimuli and they avoid sources of potential disease such as public restrooms and undercooked meat (Fessler, 2002; Fleischman & Fessler, 2011).

Moreover, many of the physiological and behavioral processes that occur during the luteal phase are mediated by increases in

☆ The data from these studies are published as a supporting online material to this paper and are available at http://psy.fsu.edu/~manerlab/pdfmail.php. This research was supported by National Science Foundation Grant BCS-1122785 awarded to the first author.

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http://dx.doi.org/10.1016/j.evolhumbehav.2013.09.001

progesterone. The luteal phase is associated with dramatic increases in progesterone: women experience increases in progesterone from the follicular phase to luteal phase that can range up to 1000% (Schultheiss, Dargel, & Rohde, 2003). During the luteal phase, the corpus luteum generates progesterone which, in turn, helps build and maintain the endometrial lining. If an egg is fertilized, progesterone levels continue to rise throughout pregnancy. Increased levels of progesterone during the luteal phase may serve as a catalyst not only for physiological changes that facilitate the growth of a fertilized egg, but also for adaptive psychological changes that could help women face challenges during pregnancy. Women's tendency to avoid potential sources of disease during the luteal phase, for example, appears to be mediated by increases in progesterone (Fleischman & Fessler, 2011).

In addition to challenges associated with immunosuppression, pregnancy also increases women's need to vigilantly avoid social threats and to recruit social allies. In many species, pregnancy hinders females' ability to locomote and the energetic costs of incubating unborn offspring reduces their capacity to pursue other goals (Ghalambor, Reznick & Walker, 2004; Kullberg, Houston, & Metcalfe, 2002; Shine, 2003). Consequently pregnant females experience reduced ability to forage for food and flee from predators and physical aggressors (Lee, Witter, Cuthill, & Goldsmith, 1996; Schwarzkopf & Shine, 1992). Indeed, throughout evolutionary history, pregnancy has involved heightened susceptibility to social threats and, as a result, it also increased women's reliance on allies who could provide resources and protection (Taylor, Klein, Lewis, Gruenewald, Gurung, & Updegraff, 2000). Consequently, psychological processes designed to avoid social threats and to nurture social alliances may arise from the increase in progesterone that occurs during the luteal phase.

2. Progesterone and social monitoring

Avoiding social threats and nurturing social alliances require a high degree of sensitivity to the social cues displayed by other people. Accordingly, heightened levels of progesterone during the luteal phase may promote early-stage perceptual attunements to a range of social cues. In line with this reasoning, we tested the hypothesis that progesterone may be a physiological catalyst for the activation of what Gardner and colleagues have termed the social monitoring system (Gardner, Pickett, & Brewer, 2000; Gardner, Pickett, Jefferis, & Knowles, 2005; Pickett, Gardner, & Knowles, 2004).

The social monitoring system is a psychological system that increases people's awareness of social cues signaling the presence of others who might help or harm them (Gardner et al., 2000; Pickett et al., 2004). When people are susceptible to threats or in need of allies, activation of the social monitoring system is up-regulated in order to quickly identify other people's interpersonal intentions. Activation of the social monitoring system is associated with heightened encoding of cues signaling possible social acceptance or social threat, such as those communicated in other people's facial expressions and vocal tones (Gardner et al., 2000, 2005; Pickett et al., 2004). By increasing sensitivity to such social cues, the social monitoring system helps people react appropriately to potential social allies or threats.

Pregnancy historically heightened women's susceptibility to social threats and increased their need for social support. Therefore, increases in progesterone during the luteal phase—a physiological process that prepares the women's bodies and minds for possible pregnancy—may cause an increase in social monitoring. Increases in social monitoring would help women adaptively navigate their social world during a time in which social interactions have especially significant consequences.

A handful of studies suggest that increases in progesterone might mediate increased processing of social cues, particularly the negative emotional signals displayed by others (Sakaki & Mather, 2012). For example, late in pregnancy when progesterone levels are especially high, women sometimes display heightened encoding of threat faces and sad faces (Pearson et al., 2009). Similarly, administration of progesterone has been shown to increase amygdala responses to angry and fearful faces (van Wingen et al., 2008; cf. Derntl, Windischberger et al., 2008b). In another study, women in the luteal phase judged disgust and fear expressions as more intense than women in the follicular phase did (Conway et al., 2007). Heightened judgments of anger and disgust in other people's faces have also been linked directly to high levels of progesterone (Derntl, Kryspin-Exner, Fernbach, Moser and Habel, 2008; Derntl, Windischberger et al., 2008). “Seeing” strong displays of anger or hostility in the faces of others could help women avoid potential sources of threat (Maner et al., 2005), a pattern that would be particularly functional when women are pregnant and especially vulnerable to danger (Taylor et al., 2000).

Thus, several studies suggest that women in the luteal phase tend to over-perceive negative emotions such as anger and disgust (Derntl, Kryspin-Exner, Fernbach, Moser and Habel, 2008; Derntl, Windischberger et al., 2008; Guapo et al., 2009). The implications of such over-perceptions for accurately detecting and decoding emotional displays are unclear. On one hand, over-perceiving negative emotions may prompt lower accuracy, as women mistake other expressions for ones signaling anger and contempt (Derntl et al., 2013). On the other hand, heightened social monitoring could result in both biased judgments (e.g., in over-interpreting expressions of anger) and increased accuracy (e.g., in initially detecting and decoding the emotions of others). Indeed, results pertaining to accuracy have been somewhat mixed. For example, one study showed that high progesterone levels biased women toward over-perceiving negative facial expressions in others, but at the same time were associated with greater accuracy in decoding the emotions experienced by other people in emotionally arousing scenarios (Derntl et al., 2013).

3. Overview of the current research

The current research extends this literature in a number of ways. First, some previous studies are limited by the fact that they did not examine the role of progesterone, instead focusing on effects of pregnancy or on differences between women in the luteal versus follicular phases. The current studies directly examined the role of progesterone using actuarial hormone estimates (Study 1) and direct salivary assays (Study 2). Second, the current studies focused on quick, initial perceptions of emotional stimuli. Many of the previous investigations described earlier assessed relatively overt social judgments. For example, some previous investigations presented participants with facial stimuli for several seconds, which could allow elaborative processing to occur (e.g., Derntl et al., 2013); thus previous findings could reflect higher-order inferences about emotions, in addition to participants' initial decoding of facial emotion. In the current studies, we assessed responses to emotional faces that were presented more quickly for 1 second (Study 1) or 500 ms (Study 2). Third, in addition to assessing the way people decode emotional displays, we examined rapid attention to emotional stimuli (Study 2). Finally, we included positive emotional expressions in Study 2 to assess the link between progesterone and attention to signs of affiliation. Although some previous studies included positive emotional expressions, processing of those stimuli sometimes demonstrated ceiling effects, making interpretation of the findings difficult (e.g., Pearson et al., 2009).

Indeed, in addition to heightening women's sensitivity to signs of pathogen avoidance and physical threat, luteal phase increases in progesterone may also be linked with psychological processes that facilitate the creation and maintenance of social alliances. Taylor and colleagues (2000) reviewed evidence that females from many species are highly motivated to “tend and befriend” social allies, especially when they are pregnant and susceptible to danger. Moreover, Taylor and others (e.g., Brown et al., 2009; Schultheiss, Wirth, & Stanton, 2004; Wirth & Schultheiss, 2006) suggest that progesterone is one key hormone that may underlie such social affiliative cognition. For example, high progesterone levels are associated with increases in women's implicit desire for social affiliation (Wirth & Schultheiss, 2006). In addition, inducing a desire for positive relationships can increase release of progesterone (Brown et al., 2009; Maner, Miller, Schmidt, & Eckel, 2010; Schultheiss et al., 2004). On luteal phase days when progesterone levels are highest, women also report increased commitment to their romantic relationships (Jones et al., 2005). Nevertheless, to our knowledge no studies have yet shown that high luteal phase progesterone levels are associated with heightened perceptual sensitivity to positive social cues.

In two studies, we tested the hypothesis that heightened luteal phase progesterone levels are associated with increased social monitoring. In two samples of women, we assessed progesterone levels using actuarial estimates (Study 1) and direct salivary assays (Study 2). We then measured women's accuracy in rapidly decoding negative facial expressions (Study 1) and women's early-stage attention to positive, negative, and neutral facial expressions (Study 2). We predicted that heightened luteal phase levels of progesterone would be linked with increased accuracy in identifying facial expressions (Study 1) and increased attention to facial expressions (Study 2).

4. Study 1

A primary function of the social monitoring system is to rapidly detect and decode social cues. Prior research demonstrates that activation of the social monitoring system is accompanied by heightened accuracy in identifying other people's facial expressions (Pickett et al., 2004). Thus, Study 1 tested the hypothesis that increases in progesterone during the luteal phase would be associated with accuracy on a facial expression identification task.

4.1. Method

4.1.1. Participants

Women who indicated during a mass screening session that they experienced regular menstrual cycles lasting approximately 28 days were e-mailed and asked to participate in a study examining menstrual cycle effects on cognition. Twenty-three normally cycling women not taking hormonal contraceptives (NC participants) and 21 women taking hormonal contraceptives (i.e., birth control pills; HC participants) participated (mean age = 19.4, SD = 2.0, range = 18–28). HC participants were included as a control group as they do not experience menstrual cycle shifts in hormones. Three HC participants did not indicate a pre- or post-session menstruation date, and one NC participant reported an abnormally short cycle (6 days); their data were excluded from analyses. Mean cycle length was 30.3 days (SD = 5.6) for NC women and 28.4 days (SD = 5.6) for HC women. Of the NC women, 10 participated during the luteal phase (day 16 through the end of cycle), 3 participated near to anticipated ovulation (days 13–15), and the remainder participated during the follicular phase (up to 12 days after onset of menstruation). Of the HC women, eight participated during the luteal phase, one participated on days 13–15, and the remainder participated during the follicular phase.

4.1.2. Procedure

Participants completed a facial expression identification (FEI) task similar to that used in previous research (Pickett et al., 2004). Stimuli included 56 pictures of 14 faces (7 male; 7 female) each displaying four emotions (anger, disgust, fear, sadness). Pictures were selected from the MacArthur Network Face Stimuli Set (http://www.macbrain.org/faces/index.htm), developed by the Research Network of Early Experience and Brain Development. Faces were displayed in random order, each for 1 second. Following the presentation of each face, participants indicated which expression they thought the face displayed by clicking one of four response options: anger, disgust, fear, sadness. Accuracy was calculated by summing the number of correct identifications. After the FEI task, participants indicated the date on which they started their last period (pre-session menstruation). Participants were instructed to email the PI when they began their next period (post-session menstruation).

4.1.3. Progesterone estimation

Based on standardized actuarial methods described in Garver-Apgar, Gangestad, and Thornhill (2008), we estimated hormone levels based on each woman's day of participation. Women's cycles were re-scaled to match a standard 28-day scale. If women participated within 14 days of the post-session menstruation date, their cycle day was calculated using the following formula: 28 − # of days between the lab session and post-session menstruation. Otherwise, cycle day was calculated using the following formula: (# of days between lab session and pre-session menstruation)/(# of days between pre-session menstruation and post-session menstruation − 14). Using estimates provided by Garver-Apgar et al (2008), we assigned each participant a progesterone value that corresponded to her standardized cycle day.

4.2. Results

Estimated progesterone levels were positively skewed. Thus, consistent with previous research (Liening, Stanton, Saini, & Schultheiss, 2010), progesterone values were log transformed. Participants, on average, correctly identified 80.3% (SD = 8.9%) of the facial expressions. Consistent with hypotheses, there was a significant correlation between estimated progesterone levels and overall FEI accuracy among NC participants ($r = .45$, $p = .037$). No such effect was observed among HC participants ($r = .10$, $p = .67$).

Additional analyses examined potential moderating effects of facial expression. Using mixed-model GLM, NC participants' FEI accuracy was predicted from progesterone estimates (continuous, between-subjects), facial expression (four levels; within-subjects), and their interaction. Corroborating the correlational analysis, the only significant effect was a main effect of progesterone [$F(1,20) = 5.02$, $p = .037$, partial $\eta^2 = .20$]. None of the effects involving facial expression approached significance (all p's > .35).

Last, we examined whether the effect of progesterone held even after controlling for other hormone levels. NC participants' FEI accuracy was regressed on progesterone estimates, as well as estrogen, testosterone, prolactin, and lh estimates (all estimated based on day of cycle; see Garver-Apgar et al., 2008). The magnitude of the progesterone effect was only slightly reduced, from zero-order ($r = .45$, $p = .037$) to semi-partial ($r = .43$, $p = .067$); none of the other hormones approached significance (all p's > .30).

Supplemental analyses examined potential moderating effects of target sex. Adding target sex as a factor revealed an interaction between target sex and facial expression [$F(3,114) = 30.55$, $p < .001$, partial $\eta^2 = .45$], such that participants were more accurate in categorizing disgust faces worn by men (compared with women), but more accurate in categorizing sadness and fear faces worn by women (compared with men); no effect of target sex was found for anger expressions. It is important to note, however, that this pattern was independent of the progesterone findings. Target sex did not moderate the relationship between progesterone and accuracy in judging facial expressions; there was no interaction between target sex, expression, and progesterone in NC women ($p > .35$) and the main effect of progesterone remained significant in NC women [$F(1,20) = 4.59$, $p = .045$, partial $\eta^2 = .19$]. Moreover, the interaction between target sex and expression was observed in both NC and HC women (both p's < .001). Thus, the effect of target expression reflected a general tendency to differentially categorize the expressions of male and female targets and did not qualify the link between progesterone and identification of facial expressions.

4.3. Discussion

Study 1 demonstrated that on days of the cycle when progesterone was estimated to be highest, women were most accurate in identifying other people's facial expressions. Thus, Study 1 findings support the hypothesis that naturally occurring increases in progesterone during the luteal phase are associated with heightened decoding of other people's emotions.

However, there were limitations to Study 1. First, although facial expression did not moderate the influence of progesterone (i.e., heightened progesterone was associated with heightened accuracy regardless of facial expression), all of the facial expressions used in Study 1 were negative. Consequently, we cannot yet rule out the possibility that progesterone is associated with increased social monitoring of only negatively valenced social cues. Second, because only social stimuli were used in Study 1, we cannot rule out the possibility that progesterone increases general awareness of all stimuli in the environment—not just those relevant for social interaction. Third, Study 1 used an indirect method for estimating progesterone levels, rather than measuring them directly. We address these limitations in Study 2. We also extend the investigation by examining another cognitive process known to reflect increased social monitoring—heightened attention to social stimuli.

5. Study 2

A key aspect of the social monitoring system is attention to socially relevant information (Gardner et al., 2000). In order to identify the intentions of other people, one must attend carefully to the social cues they display. Thus, in Study 2, women completed a visual cueing task that assessed low-level biases in attention. To address the limitations of Study 1, we measured attention to both positive and negative social stimuli (happy and angry faces), as well as non-social stimuli (household objects). We predicted that, among NC women (but not HC women), heightened levels of progesterone during the luteal phase would be associated with greater attention to social stimuli than non-social stimuli. Additionally, Study 2 incorporated a direct measurement of salivary progesterone.

5.1. Method

5.1.1. Participants

Forty-nine NC women and forty-five HC women participated (mean age = 18.6, SD = 1.04, range = 18–24). An LH surge was not observed for four NC participants, indicating the possible presence of anovulatory cycles; their data were excluded from primary analyses.

5.1.2. Procedure

NC participants were given Clearblue Easy Ovulation Digital Test Kits that measure LH in urine. A positive test signifies that an LH surge has occurred, which typically indicates that ovulation will occur within 24–36 hours (although anovulatory cycles are still possible). Four participants never received a positive result; the remaining NC participants experienced a LH surge, on average, 15.18 days (SD = 3.33 days) after the onset of menstruation.

To ensure significant variability in timing of participation, participants were randomly assigned to come into the laboratory either during the follicular phase, around ovulation, or during the luteal phase (between-subjects). NC women participated on days 5–8 after onset of menstruation (follicular phase), 0–1 after LH surge (ovulatory phase), or 5–8 days after LH surge (luteal phase). HC women participated on days 5–8 after onset of menstruation (follicular phase), 13–15 days after menstruation (mirroring ovulatory phase in NC women), and 19–22 days after menstruation (luteal phase).

To reduce diurnal variability in hormone levels, all participants arrived at the lab between 12 pm and 4 pm. To prepare for each lab session, participants refrained from activities known to affect salivary hormone measurement, including exercising, smoking, and consuming food, caffeine, or alcohol. During each session, participants provided a saliva sample by spitting into a collection vial (approximately 4 ml).

Participants performed a dot probe task used to measure attentional adhesion (Maner, Miller, Rouby, & Gailliot, 2009). Stimuli consisted of 24 neutral objects (e.g., bowls, plates) and 8 faces (4 male, 4 female) each displaying three facial expressions (smiling, angry, neutral) that were used in previous research (DeWall et al., 2009). On each trial of the dot probe task, a fixation cross first appeared in the center of the computer screen for 1000 ms. Next, a target stimulus was displayed for 500 ms in one quadrant of the computer screen (upper left, upper right, lower left, lower right). Immediately following the disappearance of that stimulus, a categorization object (a circle or square) appeared in either the same location as the target stimulus (“filler trials”) or in a different location (“attentional shift trials”). Participants indicated via key press as quickly and accurately as possible whether the categorization object was a circle or square. Greater latencies on attentional shift trials indicated that participants took longer to disengage their attention from the target stimulus (i.e., more attentional adhesion). After completing a block of practice trials, participants completed four blocks of experimental trials. Each block consisted of 24 trials (6 “filler” and 18 “attentional shift”). The order in which stimuli and trials appeared was randomized across participants.

Due to software error, trial accuracy was not recorded. Thus, we could not remove trials with incorrect responses. However, other research using versions of this dot probe task reported incorrect responses on only a small percentage of trials (less than 5%; Maner et al., 2007, 2009). Moreover, including incorrect trials should add only error variance, thus making any statistical tests more (rather than less) conservative.

5.1.3. Progesterone measurement

Saliva samples were frozen at −20 °C. To precipitate mucins, samples were thawed and centrifuged at 4000 rpm for 10 min. The supernatant was stored at −20 °C until assayed. Commercially available solid-phase Coat-A-Count ^{125}I radioimmunoassay kits provided by Siemens Medical Solutions Diagnostics (Los Angeles, CA) were used to measure concentrations of progesterone. Each sample contained 400 μl of participant supernatant. Standards and controls were diluted (1:40) with distilled water (analytical range: 2–1000 pg/ml). Tubes were incubated for 20 hours after adding radio-labeled tracer. All samples were processed in duplicate using a high-throughput, automated gamma counter. The intra- and inter-assay CVs were 17.1% and 13.7%, respectively, which are commensurate with previous salivary measurements of progesterone (Liening et al., 2010; Wirth, Meier, Fredrickson, & Schultheiss, 2007).

5.2. Results

5.2.1. Preliminary analyses

Progesterone values were positively skewed and thus were log transformed. One NC participant in the follicular phase had an extremely high progesterone value (greater than 3 SD above the mean NC follicular phase value, possibly indicating a contaminated sample); her data were excluded from analyses. Table 1 presents mean (non-transformed) salivary progesterone levels by phase of cycle among NC participants and HC participants separately.

Table 1
Study 2: Mean (SD) salivary progesterone values (pg/ml) by phase of the cycle among normally cycling participants (NC) and participants on hormonal contraceptives (HC).

	NC participants ($n = 44$)	HC participants ($n = 45$)
Follicular phase	11.9 (7.9)	10.7 (3.5)
Ovulatory phase	18.5 (7.3)	11.5 (7.8)
Luteal phase	88.5 (53.8)	9.9 (8.9)

Consistent with hormonal changes across the menstrual cycle, NC participants' progesterone levels varied substantially by cycle phase [$F(2,41) = 22.02$, $p < .001$, partial $\eta^2 = .52$]. NC participants had substantially higher progesterone levels during the luteal phase than the follicular phase [$F(1,41) = 40.47$, $p < .001$, partial $\eta^2 = .50$] and ovulation [$F(1,41) = 19.21$, $p < .001$, partial $\eta^2 = .32$]. NC participants' progesterone levels were somewhat higher around ovulation than the follicular phase [$F(1,41) = 3.37$, $p = .074$, partial $\eta^2 = .08$]. There was no effect of cycle phase on HC participants' progesterone levels [$F(2,42) = 1.94$, $p = .16$], consistent with data demonstrating that oral contraceptives inhibit the secretion of endogenous progesterone and that salivary assays lack sensitivity to exogenous gestagens (Schultheiss et al., 2003).

5.2.2. Dot probe task

The reaction time (ms) with which participants responded on attentional shift trials served as the dependent variable. Trials with latencies greater than three standard deviations above/below the participant's mean latency were excluded from analyses. On average, only 1.5% (SD = 1.2%) of trials were excluded. One HC participant had an unusually high average response time (greater than 3 SD above the sample mean), suggesting that she did not follow task instructions; her data were excluded from analyses.

GLM analyses were performed separately among HC and NC participants. Reaction time on attentional shift trials was predicted from stimulus type (social versus non-social, within-subjects), progesterone values (a continuous between-subjects factors), and their interaction. No significant effects were observed among HC participants. Among NC participants, there were significant main effects of progesterone [$F(1,42) = 5.38$, $p = .025$, partial $\eta^2 = .11$] and stimulus type [$F(1,42) = 6.47$, $p = .015$, partial $\eta^2 = .13$]. However, these were qualified by the predicted interaction between progesterone and stimulus type [$F(1,42) = 4.30$, $p = .044$, partial $\eta^2 = .09$]. As seen in Figure 1, NC participants high in progesterone (1 SD above the mean) attended more to social stimuli than non-social stimuli [$F(1,42) = 10.65$, $p = .002$, partial $\eta^2 = .20$]; NC participants low in progesterone (1 SD below the mean) displayed no difference in their attention to social and non-social stimuli ($F < 1$). Additionally, among NC participants, progesterone was significantly correlated with attention to social stimuli ($r = .37$, $p = .015$; replicating Study 1), and only more weakly correlated with attention to non-social stimuli ($r = .29$, $p = .054$). Nevertheless, given that progesterone was (marginally) associated with attention to non-social stimuli, we performed additional analyses to assess further whether the link with progesterone was stronger for social stimuli: when controlling for attention to neutral objects, the association between progesterone and attention to faces was only slightly reduced and remained marginally significant (partial $r = .27$, $p = .086$). In contrast, controlling for attention to faces greatly reduced the association between progesterone and attention to neutral objects (partial $r = -.14$, $p = .37$). (Neither of these partial correlations approached significance among women on hormonal birth control.) Thus, these results suggest that luteal phase increases in progesterone were uniquely associated with attention to social stimuli.

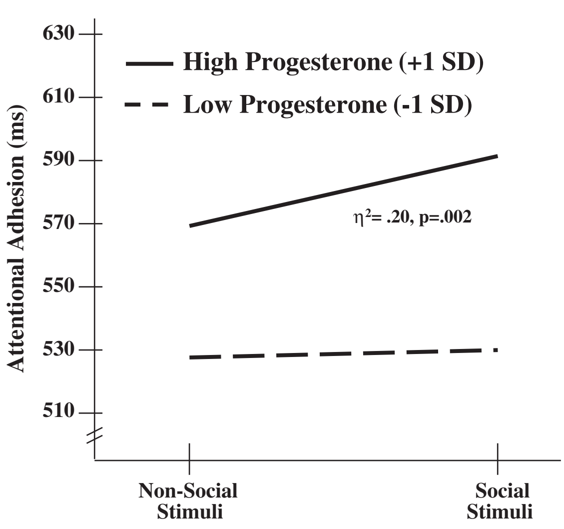

Fig. 1. NC participants high in progesterone (1 SD above the mean) attended more to social stimuli than non-social stimuli. NC participants low in progesterone (1 SD below the mean) showed no difference in attention to social and non-social stimuli.

Supplemental analyses examined potential moderating effects of facial expression. Using mixed-model GLM, NC participants' reaction time on attentional shift trials to social stimuli was predicted from target expression (happy vs. angry vs. neutral; within-subjects), progesterone level, and their interaction. We again observed a main effect of progesterone [$F(1,42) = 6.56$, $p = .014$, partial $\eta^2 = .14$], which was *not* moderated by target expression (i.e., the interaction between progesterone and target expression did not approach significance, $F < 1$). Indeed, progesterone levels were correlated to an equivalent degree with attention to happy faces ($r = .34$, $p = .025$), angry faces ($r = .38$, $p = .012$), and neutral faces ($r = .34$, $p = .023$). Thus, effects of progesterone were observed across positive, negative, and neutral facial expressions. There was also a main effect of target expression [$F(2,41) = 3.26$, $p = .048$, partial $\eta^2 = .14$]. Participants attended more to neutral faces ($M = 567$, SD = 84) than happy faces [$M = 554$, SD = 85; $F(1,42) = 5.34$, $p = .026$, partial $\eta^2 = .11$] and angry faces [$M = 556$, SD = 90; $F(1,42) = 3.18$, $p = .082$, partial $\eta^2 = .07$]; there was no difference between happy and angry faces ($F < 1$).

5.3. Discussion

Study 2 provides evidence for a relationship between heightened luteal phase progesterone and increases in attention to social stimuli (faces). Normally cycling women's progesterone levels were associated with attentional adhesion to social stimuli (conceptually replicating Study 1). Moreover, progesterone levels were more robustly associated with attentional adhesion to social stimuli than non-social stimuli. Consistent with Study 1 findings, this effect was not moderated by facial expression, nor was it was observed among women taking oral contraceptives. Thus, findings are consistent with the hypothesis that increases in progesterone during the luteal phase are accompanied by general increases in social monitoring.

Although we found no moderating effects of facial expression, we did find a main effect such that participants attended more strongly to neutral faces than to happy or angry faces. Previous findings on attention to emotional expressions have been mixed. Although several studies suggest that angry faces are detected more quickly than other expressions (Fox et al., 2000), recent work suggests that happy faces are actually detected more quickly (Becker, Anderson, Mortensen, Neufeld and Neel, 2011), especially when people are motivated to form social bonds (DeWall et al., 2009). One might speculate that the strong attentional adhesion to neutral faces in the current study could reflect the fact that neutral faces are inherently ambiguous and thus may capture attention because the interpersonal intentions communicated by the face are unclear.

6. General discussion

Across two studies, heightened luteal phase progesterone levels were associated with increased accuracy in decoding others' facial expressions (Study 1) and increased attention to social stimuli (Study 2). Both processes reflect activation of the social monitoring system, which attunes individuals to the opportunities and threats afforded by other people. These findings suggest that people's perceptual sensitivity to social information is guided, in part, by naturally occurring endocrinological changes relevant to reproductive success.

These findings add to a rapidly growing literature suggesting that women's psychology and behavior fluctuate adaptively across the menstrual cycle (Gangestad, Thornhill, & Garver-Apgar, 2005). The majority of the recent literature has focused on ovulation and mating, revealing for example that women display heightened attraction to highly dominant or genetically fit men around ovulation in order to maximize reproductive benefits associated with peak levels of fertility (e.g., Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Macrae, Alnwick, Milne & Schloerscheidt, 2002; Penton-Voak et al., 1999).

The current findings, in contrast, add to a smaller body of literature examining psychological processes associated with the luteal phase (e.g., DeBruine, Jones, & Perrett, 2005; Fleischman & Fessler, 2011; Jones et al., 2005). The current research extends this literature by demonstrating that luteal phase increases in progesterone—a hormone that plays a key role in facilitating fertilization and pregnancy—are associated with sensitivity to social stimuli signaling a high likelihood of social affiliation or social threat. Just as psychological changes that occur around ovulation appear to serve specific mating-related functions, some of the psychological changes that occur during the luteal phase may serve specific affiliative and self-protective functions. This view fits with most evolutionary perspectives, which emphasize the domain-specificity of psychological mechanisms (Barrett & Kurzban, 2006).

Although participants in these studies were not pregnant, the logic of our conceptual framework implies that progesterone evokes heightened social monitoring because high progesterone levels in the luteal phase prepare the woman for possible pregnancy and because the careful processing of social cues would have been especially adaptive during pregnancy (cf. Taylor et al., 2000). This is conceptually similar to pathogen avoidance processes during the luteal phase. Regardless of whether or not women have actually conceived, women's immune systems are suppressed in order to avoid rejecting a growing fetus and high luteal phase progesterone therefore prompts women to avoid pathogen sources during this period (Fleischman & Fessler, 2011). Although heightened social monitoring could reflect a byproduct of progesterone's link with pregnancy, it might also be the case that cyclical shifts in social monitoring are adaptive because such shifts would help women prepare for possible pregnancy should it occur. This would follow an error management approach (Haselton & Buss, 2000). Just as women's bodies prepare for pregnancy (regardless of whether fertilization has occurred) during the luteal phase by creating the corpus luteum and by temporarily suppressing immune system function, so too might women's psychology help prepare them for possible pregnancy by firming up social resources and avoiding social danger.

The current findings also add to an emerging literature demonstrating the importance of evolved goals for shaping early-in-the-stream cognitive processing (Ackerman et al., 2009; Anderson et al., 2010; Maner et al., 2009; Miller, Maner, & Becker, 2010). The dependent measures used in this research reflect the operation of low-level perceptual processes—processes that provide the basic building blocks for higher-order cognition and behavior. The stimuli people are sensitive to at early stages of cognition influence what information is encoded, remembered, and integrated into their behavior. The current research, therefore, provides a relatively direct window into the lower-order cognitive consequences of naturally shifting levels of progesterone—consequences that could have a profound influence on adaptive forms of social behavior.

In the current research, high progesterone levels were associated with increased sensitivity to social stimuli, regardless of the specific benevolent or agonistic intentions communicated by those stimuli. However, the content of those intentions might still moderate the effect of progesterone on more downstream levels of cognition. For example, Conway et al. (2007) found that when progesterone peaked during the luteal phase, women subjectively judged as more intense the emotional expressions displayed by others indicating nearby threat (e.g., disgust and fear expressions), but progesterone levels were unassociated with the perceived intensity of happy expressions (see also Pearson et al., 2009). Similarly, Derntl, Kryspin-Exner, Fernbach, Moser and Habel (2008) and Derntl, Windischberger et al. (2008) observed that, when they were provided substantial time to scrutinize another person's facial expression (unlike Study 1 of the current research in which the expression was displayed for only 1 second), heightened progesterone biased women toward judging faces as expressing anger and disgust (i.e., over-perceiving cues of potential threat). Thus, although heightened progesterone during the luteal phase may involve an initial sensitivity to a wide range of social stimuli, once social information is encoded, more downstream stages of cognition may involve preferential processing of negative social cues. This would be consistent with previous work demonstrating that the same set of social motives can exert different effects at different stages of cognition (Ackerman et al., 2009; Becker et al., 2010). Nevertheless, the overall literature on progesterone has provided relatively greater evidence for enhanced threat processing than processing of affiliative cues. Future research is needed to more fully delineate the ways in which progesterone promotes sensitivity to people who provide opportunities for social affiliation.

Future research would also benefit from more carefully assessing other hormones, as well as numbers of hormone receptors, that might affect social information processing. Although the current findings implicate progesterone as one factor underlying sensitivity to social information, the findings are not definitive in ruling out effects of other hormones or potential interactions among hormones. For example, recent work suggests that effects of testosterone on social dominance processes sometimes are moderated by levels of cortisol (Mehta & Josephs, 2010). Studies would benefit from assessing whether similar interactions apply to progesterone's effects on the processing of social cues. Future studies would also benefit from assessing potential effects associated with different forms of hormonal birth control. Different contraceptives involve different doses and types of progesterone (and estrogen) and may disrupt normal cyclical shifts across the menstrual cycle in different ways (Cobey, Pollet, Roberts and Buunk, 2011; Welling et al., 2012). Moreover, it is important to recognize that the effects reported in this research were observed as a function of endogenous (as opposed to exogenous/ingested) progesterone.

In addition, both of the current studies are limited by their reliance on between-subjects designs. Thus, we were not able to assess cyclic changes that occur within individual women. Future research would benefit from using within-subjects designs to assess changes in social monitoring across the menstrual cycle. Both of the current studies also were limited by the reliance on relatively small samples. Although the replication across studies increases confidence in the reliability of these findings, future studies would benefit from employing larger samples.

Throughout history, pregnancy has presented women with a variety of important social challenges. Consequently, evolutionary scholars have proposed that women may possess adaptive mechanisms designed to help them face those challenges. The current studies suggest that luteal phase increases in progesterone may serve as one mechanism that helps women face adaptive challenges associated with pregnancy. Findings suggest that high levels of progesterone were associated with accurate decoding of and attention to a range of social cues—perceptual sensitivities that could help women recruit social allies and avoid social threats. Future studies would benefit from further investigating the potentially adaptive psychological effects of progesterone. At a broader level, studies would benefit from continuing to integrate theories from evolutionary psychology, behavioral endocrinology, and social cognition.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.09.001

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