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Journal
Neurobiology of Learning and Memory, 106(2013)

ISSN
1074-7427

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Publication Date
2013-11-01

DOI
10.1016/j.nlm.2013.07.015

Peer reviewed

Published in final edited form as:
Neurobiol Learn Mem. 2013 November ; 106: . doi:10.1016/j.nlm.2013.07.015.

Sex and menstrual cycle phase at encoding influence emotional memory for gist and detail

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Abstract

Sex influences on emotional memory have received increasing interest over the past decade. However, only a subset of this previous work explored the influence of sex on memory for central information (gist) and peripheral detail in emotional versus neutral contexts. Here we examined the influence of sex and menstrual cycle phase at encoding on memory for either an emotional or neutral story, specifically with respect to the retention of gist and peripheral detail. Healthy naturally cycling women and men viewed a brief, narrated, three-phase story containing neutral or emotionally arousing elements. One week later, participants received a surprise free recall test for story elements. The results indicate that naturally cycling women in the luteal (high hormone) phase of the menstrual cycle at encoding show enhanced memory for peripheral details, but not gist, when in the emotional compared with neutral stories ($p<.05$). In contrast, naturally cycling women in the follicular (low hormone) phase of the menstrual cycle at encoding did not show enhanced memory for gist or peripheral details in the emotional compared with neutral stories. Men show enhanced memory for gist, but not peripheral details, in the emotional versus neutral stories ($p<.05$). In addition, these sex influences on memory cannot be attributed to differences in attention or arousal; luteal women, follicular women, and men performed similarly on measures of attention (fixation time percentage) and arousal (pupil diameter changes) during the most arousing phase of the emotional story. These findings suggest that sex and menstrual cycle phase at encoding influence long term memory for different types of emotional information.

Keywords

Sex differences; menstrual cycle; emotional memory; gist; detail; eye-tracking

1. Introduction

It is well established that emotionally arousing events tend to be better remembered than neutral events (Bradley, Greenwald, Perry and Lang, 1992; Cahill and McGaugh, 1995; 1998; McGaugh, 2000). Substantial evidence since the 1970's from both animal and human subject literature indicates that adrenal hormones (i.e. catecholamines and glucocorticoids) released during or after emotionally arousing events strongly influence the consolidation of

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long term memories (McGaugh and Roozendaal, 2002). These adrenal hormones interact to enhance memory consolidation for emotional experiences via actions involving the amygdala, a brain region believed to be critical for the modulation of memory consolidation (Roozendaal, McEwen, and Chattarji, 2009; McGaugh, Cahill, Roozendaal, 1996; Roozendaal, Cahill, and McGaugh, 1996b).

Research also suggests that emotional memory is influenced by sex hormones, particularly ovarian hormones (eg, Andreano, Arjomandi, and Cahill, 2008). Previous research examined whether sex differences in emotional memory could be influenced by menstrual cycle-related changes in sex hormone levels. Some studies have explored how sex and stress hormones interact to influence memory performance (Andreano, Arjomandi, and Cahill, 2008), whereas other recent studies suggested that progesterone levels can influence emotional memory, even in the absence of a post-training stressor. Ertman et al. (2011) examined whether naturally cycling women in hormonally distinct phases of the menstrual cycle differentially recalled emotional images one week after encoding. Enhanced recall of emotional images was only observed in women in the luteal (high hormone) phase of the menstrual cycle; furthermore, regression analyses revealed a positive correlation between memory and progesterone levels at encoding (Ertman, Andreano, and Cahill, 2011).

Human imaging studies have provided additional evidence that sex hormones influence memory. van Wingen and colleagues (2008) demonstrated that high levels of synthetic progesterone increased amygdala responses to emotional images relative to neutral images. These findings were further supported by a study examining the influence of sex hormones on amygdala and hippocampal activity, in which women in the mid-luteal phase exhibited an enhanced response to emotional images in the hippocampus and amygdala as compared to women in the early follicular phase (Andreano and Cahill, 2010). These findings suggest that sex hormones modulate the responsiveness of a key node in the brain's emotional memory circuitry – the amygdala.

Additional imaging studies have explored sex influences on the amygdala during emotionally arousing tasks, irrespective of sex and stress hormone levels. For example, several studies have reported a sex-related hemispheric lateralization of amygdala activity in relation to long-term emotional memory (e.g., Andreano and Cahill, 2009). Cahill and colleagues (2001) found that activity of the right hemisphere amygdala in men viewing emotional stimuli was significantly correlated with long-term recall of the stimuli; there was no relationship with the left hemisphere amygdala. However, activity in the left hemisphere, but not the right, amygdala in women viewing emotional stimuli was significantly related to long-term recall. This relationship was replicated in different paradigms investigating sex influences on emotional memory (Canli, Desmond, Zhao, and Gabrieli, 2002; Cahill, Uncapher, Kilpatrick, Alkire, and Turner, 2004; Mackiewicsz, Sarinopoulos, Cleven, and Nitschke, 2006). A subsequent study by Kilpatrick and colleagues (2006) demonstrated that a sex-related hemispheric lateralization of amygdala function exists even when men and women are resting, a finding strongly confirmed by Savic and Lindstrom (2008).

Several studies expanded upon this sex-related hemisphere laterality of amygdala function to examine sex influences on emotional information processing. There is evidence for a hemispheric specialization in the processing of global (gist) versus local (detail) information from an event; the right hemisphere is associated with the processing of gist whereas the left hemisphere is associated with detail processing (Fink, Halligan, Marshall, Frick, Frackowiak, and Dolan, 1996; Fink, Marshall, Halligan, and Dolan, 1999). Cahill and van Stegeren (2003) integrated these hemispheric laterality findings to test the hypothesis that a β-adrenergic blocker, by presumably impairing the amygdala's modulatory effects on memory, should impair memory for gist of an emotionally arousing story in men (by

impairing right amygdala/hemisphere functions) but memory for details of the same story in women (by impairing left amygdala/hemisphere functions). Results from the study supported the hypothesis.

Potential sex influences on memory for central information (gist) and detail from an emotional event have been explored in several studies (Cahill and van Stegeren, 2003; Cahill, Gorski, Belcher, and Huynh, 2004; Seidlitz and Diener, 1998). Recently, we reported that women taking hormonal contraception had enhanced memory for the gist, but not for the details, of an emotional story, whereas naturally cycling women had enhanced memory for the details, but not gist (Nielsen, Ertman, Lakhani, and Cahill, 2011). These findings suggest that sex hormones influence the retention of gist versus detail from an emotional event. To date, however, potential effects of menstrual cycle at encoding on retention of gist and detail remain unexamined.

The present study investigated memory for gist and detail of an emotional story in naturally cycling women as well as in men, specifically focusing on the influence of menstrual-cycle related sex hormone fluctuations at encoding. Women on hormonal contraception were not included in this study since the focus was on the relationship between emotional memory for gist and detail and endogenous sex hormones.

Based on our previous study (Nielsen et al., 2011), we predicted that naturally cycling women in the *high sex hormone*, or luteal, phase of the menstrual cycle would exhibit enhanced memory for the total details of an emotional story as well as details from the most emotional phase, "phase 2;" more specifically, based on previous work with sex hormones and emotional memory, we predicted that higher levels of progesterone would relate to enhanced retention of detail memory. We also hypothesized that both women in the follicular, or *low sex hormone*, phase of the menstrual cycle and men would not show enhanced memory for emotional story details (Cahill and van Stegeren, 2003; Nielsen et al., 2011).

2. Materials and methods

2.1 Participants

Eighty-nine naturally cycling (NC) female and forty-three male undergraduate students from the University of California, Irvine between the ages of 18–33 participated in this study, which was approved by the university's Institutional Review Board. The subjects received course credit for their participation in the study. Participants were asked to refrain from alcohol, caffeine, and cardiovascular exercise for twenty-four hours prior to each experimental session to control for outside influences that could affect baseline stress hormone levels. To avoid contamination of salivary samples, participants were asked to fast one hour prior to each experimental session as well as refrain from brushing teeth within the hour before their appointment.

Of the participants, 20 naturally cycling women were excluded due to irregular menstrual cycles (i.e. inconsistent menstruation patterns, 13), failure to return for the second experimental session (5), progesterone levels three standard deviations above the mean (1), or nursing (1). Ten naturally cycling women were also excluded for having progesterone and 17β-estradiol levels well outside of the expected hormone ranges (6 Luteal, 4 Follicular). Four men were excluded based on their failure to return for the second experimental session (2), having neutral recall scores more than three standard deviations above the mean (1), or taking more than three prescription medications (1). Of the participants included in the final analyses, six participants reported using one or two prescription medications (3 men, 1 follicular woman, 2 luteal women). The final analyses included data from 59 NC women

and 39 men. The NC women were further divided into a “follicular” group (1–14 days from the start of menstruation) or a “luteal” group (15–30 days from the start of menstruation) (Azziz, Hincapie, Knochenhauer, Dewailly et al., 1999; Franklin, Ehrman, Lynch, Harper, Sciortino, O'Brien, and Childress, 2008; Sakaki and Mather, 2012; De Bondt, Van Hecke, Veraart, Leemans, Sijbers, et al., 2013). We used a forward day count from the first day of menstruation to determine menstrual cycle position, and all women included in these analyses had progesterone and 17β-estradiol levels within the expected hormone ranges (Salimetrics, State College, PA). Of the NC women, 28 women were in the follicular phase of the menstrual cycle, and 31 women reported being in the luteal phase at the time of encoding.

2.2 Procedures

All experimental sessions were conducted between the hours of 12:00 and 18:00 to control for the effects of circadian rhythm on salivary alpha amylase and cortisol levels. During the first experimental session, participants filled out a screening questionnaire and three cognitive assessments including the BEM Sex Roles Inventory (BEM; Bem, 1981), the Positive and Negative Affect Schedule (PANAS; Watson, Clark, and Tellegen, 1988), and the Mehrabian test (Mehrabian, 1994). The BEM was implemented to assess masculine and feminine influences/traits within each individual participant, whereas the PANAS was given to measure the participants' affect at the time of testing. The Mehrabian was implemented to assess levels of trait anxiety (Mehrabian, 1994). These questionnaires were implemented to standardize the activities between each participant's arrival and their baseline sample; scores from these questionnaires were not analyzed with respect to memory.

Fifteen minutes after their arrival, participants provided a 1-mL saliva sample using the “passive drool” collection method. Following the baseline saliva sample, participants underwent a 5-pt. calibration on the iView X RED eye-tracking system (SensoMotoric Instruments).

Participants then viewed either a brief, narrated story containing emotionally arousing elements or one containing only neutral elements. Each version of the story was composed of 11 slides, and the images on the slides were identical between the two versions of the story. The stories were also identical in the narratives associated with slides 1–4 or “phase 1” and similar in those associated with slides 9–11 or “phase 3” of the slideshow. However, the stories were quite different in the narratives associated with slides 5 – 8 or “phase 2;” in this part of the story, the emotional version contained the most emotionally arousing elements unlike the neutral version of the story.

Immediately after the slide show, participants were asked to rate the story on a 1 – 9 scale of emotional arousal; 1 = “not at all emotionally arousing” and 9 = “extremely emotionally arousing.” Participants were free to rate the story using any of the numbers between 1 and 9. Also, participants provided a second 1-mL saliva sample. An additional sample was taken fifteen minutes after termination of the slide show.

One week later, participants returned and provided one 1-mL saliva sample after a fifteen minute acclimation period. This sample was taken to maintain consistency between the experimental sessions and was not analyzed for 17β-estradiol, progesterone, or testosterone levels. A surprise free recall test for slide recall and associated story elements was administered shortly after the saliva sample. During the test, subjects were asked to write a brief phrase identifying each slide they remembered as well any elements of the story they could recall that were associated with each remembered slide. After completing the test, subjects were debriefed and compensated with course credit.

2.3 Scoring of Recall Performance

Correct recall of a slide was credited if the identifying phrase used by the subject could unambiguously be attributed to a specific slide. Slide descriptions not clearly linked to a picture in the slide show were not counted. The vast majority of responses unambiguously identified a particular slide. A scoring template derived from our previous work with these stories (Nielsen et al., 2011; Cahill & van Stegeren, 2003; Cahill, Gorski, Belcher, & Huynh, 2004) was used to score recalled story elements as concerning either the "gist" or "details" of the story. In these previous studies, "gist" was defined by a consensus of ¾ independent judges as "any story element that could not be changed or altered without changing the fundamental story line" (Cahill & van Stegeren, 2003). In the scoring template used here and elsewhere (Nielsen et al., 2011), scored gist items reflect those determined to be "gist" by the independent judges in previous work (Cahill and van Stegeren, 2003). Gist items were derived from both the narrative and slides and the number that could be recalled varied by slide. Examples of gist items from the scoring template for phase 2 of the emotional version include "boy hit by a runaway car," "boy critically injured," and "the boy is taken to a nearby hospital."

"Details" were defined as all other recalled elements and the number of details that could be recalled differed by slide (Cahill & van Stegeren, 2003). Examples of detail items from the scoring template for phase 2 of the emotional story include "hospital – light brown," "parked car in background," and "boy post-surgery."

Of the slides that were correctly recalled, the associated story elements were scored as either a "gist" or "detail" if the story element corresponded to a "gist" or "detail" item on the scoring template. Most of the story elements listed by the subjects (85%) were classifiable by this method as either "gist" or "detail." Recall performance was scored by two independent judges. Agreement between the two judges was 97%. The relatively few cases of disagreement were decided by a third independent judge.

2.4 Eye Movements and Pupil Dilation

Fixation duration and pupil dilation were measured using the iView X RED eye-tracking software at a sampling rate of 120 Hz. We selected these measures for analysis because fixation time has been used as an index of attention and visual processing (Dalton et al., 2005), and pupil dilation is considered a reliable measure of arousal (Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Einhauser, Stout, Koch, & Carter, 2008). Standard analysis procedures were used (Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Einhauser, Stout, Koch, & Carter, 2008). Fixation and pupil dilation data for each participant were exported using the eye-tracking analysis software program BeGaze 2 (SensoMotoric Instruments). Eye movement events (fixations, saccades, blinks) for the duration of each slide (approximately 15 seconds) were exported. Fixation time % was determined by adding the time of each fixation event within a slide and dividing the total fixation time by the total time of the slide; this was determined for each slide (data not shown) and each phase.

In order to examine whether luteal women, follicular women, and men visually explored the slides differently, we conducted an area of interest (AOI) analysis on two of the most emotional and visually complex slides of phase 2 of the emotional story (Poole & Ball, 2005). We selected four AOIs between the two slides. Within each AOI, we examined the number of glances (entries) the subject made into the area as well as the number of fixations made upon entry.

In between each slide, a grayscale image matched for luminance appeared for 3 s to control the level of illumination prior to picture onset (Bradley et al., 2008). Average pupil dilation was calculated for each image using methods adopted from Bradley et al. (2008); the

average baseline diameter in the 3 s before the image presentation was subtracted from the average pupil diameter in the 3 s following the offset of the narration. This approach was necessary because in this paradigm, the visual images in both the emotional and neutral stories were identical (Cahill, Prins, Weber, and McGaugh, 1994). The emotional response to each slide is determined by the narrative in the slide. Thus, the most appropriate method for assessing an arousal response to each slide is to assess pupil dilation before and after the slide's narration.

2.5 Saliva Samples

Saliva samples were immediately frozen for a minimum of twenty-four hours to allow mucins to precipitate. Prior to the assays, they were thawed and centrifuged at 2,080 × g for 15 minutes to extract particulates from saliva. Samples were then centrifuged a second time at 2,080 × g for 10 minutes to extract any additional particulates from saliva. Clear supernatant was decanted into microtubes.

2.6 Salivary Measurement of Sex Steroid Hormones

Salivary levels of 17β-estradiol, progesterone, and testosterone were measured using Salimetrics (State College, PA) ELISA kits and measured optically using BioTek Instruments, Inc. ELx808 Absorbance Microplate Reader (Winooski, VT). In naturally cycling women, we assayed two saliva samples for 17β-estradiol, progesterone, and testosterone; from these samples, we determined the average levels of these hormones. In men, we assayed two saliva samples for testosterone and determined the average testosterone level for each participant. The saliva samples selected for the assays were those taken at baseline and fifteen minutes post-slideshow. We used the assays to determine whether women were within the expected range for each menstrual cycle phase, and to assess overall group differences between follicular and luteal women. Mean values of 17β-estradiol and progesterone were within the expected ranges of the used assays for both follicular and luteal women (Salimetrics, State College, PA).

2.7 Statistical Analysis

We used correlation analyses to determine the relationship between levels of sex steroid hormones and recall of gist and detail in all three groups. One-way ANOVAs were used to analyze differences in PANAS, BEM, and Mehrabian test scores between luteal women, follicular women and men; we also used a 3 × 3 × 2 ANOVA, 3 × 2 ANOVAs and one-way ANOVAs to assess differences in slide recall and gist and detail recall in the emotional and neutral stories in the three groups of participants.

3. Results

3.1 Participants

Men (M = 20.33, SD = 2.8), follicular women (M = 20.0, SD = 2.1), and luteal women (M = 20.2, SD = 1.7) did not differ significantly in age. A chi-square test of independence also determined that the three groups did not differ significantly in ethnicity, $X^2(6, n = 98) = 3.05$, *n.s.*

3.1.1 Sex Hormone Levels and Menstrual Cycle Position—Menstrual cycle position in naturally cycling women was determined by self-report and verified using salivary hormonal assays. Luteal women had significantly higher levels of progesterone ($F_{(1, 57)} = 17.21$, $p < .0001$; see Fig 1a) and 17β-estradiol ($F_{(1, 57)} = 18.25$, $p < .0001$; see Fig 1b) compared to follicular women. We also examined salivary testosterone levels in men and women in both phases of the menstrual cycle; men had significantly higher levels of

testosterone ($F_{(1, 96)} = 126.96$, $p < .0001$; see Fig 1c) than both follicular and luteal women, who did not differ from one another.

3.1.2 Emotional Arousal Ratings and Cognitive Questionnaires—There were no significant differences in arousal ratings for the emotional ($F_{(2,47)} = 1.15$, $p > 0.1$) or neutral ($F_{(2,45)} = 1.27$, $p > 0.1$) stories between the three groups (men vs. follicular women vs. luteal women). Men ($F_{(1,37)} = 48.94$, $p < .0001$), follicular women ($F_{(1, 26)} = 27.8$, $p < .0001$), and luteal women ($F_{(1,29)} = 22.4$, $p < .0001$) all rated the emotional story as significantly more emotionally arousing than the neutral story.

Participants were given three cognitive questionnaires prior to the start of the experiment. Men, follicular women and luteal women scored significantly differently on the Positive Affect component of the PANAS ($F_{(2,95)} = 3.4$, $p < .05$), the BEM ($F_{(2, 95)} = 8.5$, $p < .001$), and the Mehrabian ($F_{(2, 95)} = 3.7$, $p < .05$). Group means ± SEM are outlined in Table 1.

3.2 Memory findings

3.2.1 Slide Recall—We first considered the total recall of all slides from the emotional and neutral stories. A 3 × 2 ANOVA for total slide recall with menstrual phase at encoding (men vs. follicular vs. luteal) and emotional story content as independent factors revealed a main effect of emotion on slide recall ($F_{(1, 96)} = 17.7$, $p < .0001$). The main effect of menstrual cycle phase at encoding ($F_{(2,95)} = .03$, $p >> 0.1$) and the interaction effect of emotion × menstrual cycle phase at encoding ($F_{(2, 95)} = 0.04$, $p >> 0.1$) were non-significant. Men ($F_{(1, 37)} = 8.62$, $p < .01$), follicular women ($F_{(1, 26} = 6.02$, $p < .05$), and luteal women ($F_{(1, 29)} = 7.6$, $p = .01$) all recalled significantly more slides from the emotional relative to the neutral story (Fig 2).

As predicted based on previous work with this story paradigm, the enhancement of total slide recall was driven by enhanced slide recall from the emotional component of the emotional story (phase 2). A 3 × 2 ANOVA with menstrual phase at encoding and emotional story content as independent factors showed that all three groups recalled significantly more phase 2 slides from the emotional compared with neutral stories ($F_{(1, 96)} = 19.1$, $p < .0001$). The main effect of menstrual phase at encoding ($F_{(2, 95)} = 0.19$, $p >> 0.1$) and the interaction effect of emotion × menstrual cycle phase ($F_{(2, 95)} = .08$, $p >> 0.1$) were non-significant.

3.2.2 Recall of Gist and Detail—In analyzing gist and detail, we first considered total gist and detail retention from the emotional and neutral stories. A 3 × 2 ANOVA for total gist recall with menstrual phase at encoding (luteal v. follicular v. men) and emotional story content (emotional v. neutral) as independent factors revealed a main effect of emotion on total gist recall ($F_{(1, 96)} = 8.0$, $p < .01$). The main effect of menstrual cycle phase at encoding and the interaction effect of emotion × menstrual cycle phase at encoding were non-significant.

We also assessed total detail memory using a 3 × 2 ANOVA with menstrual phase at encoding and emotional story content as independent factors. There was a main effect of emotion on total detail recall ($F_{(1, 96)} = 8.1$, $p < .01$); however, the main effect of menstrual cycle phase at encoding and the interaction effect of emotion × menstrual cycle phase at encoding were non-significant.

Given that there was an effect of emotion on total gist and detail recall, we further examined total gist and detail memory in all three groups using a series of one-way ANOVAs. Although all three groups displayed an emotional memory enhancement for total slide recall, they exhibited different memory for gist and detail from the emotional story. As predicted based on prior work (Cahill and van Stegeren, 2003), men recalled significantly more gist

($F_{(1, 37)} = 5.34$, $p < .05$; see Fig 3a) from the emotional ($M = 5.67$, $SD = 2.76$) compared to the neutral story ($M = 3.67$, $SD = 2.61$). However, men recalled details no differently in the emotional compared to the neutral story.

For naturally cycling women, the pattern of gist and detail recall from the emotional story differed depending on menstrual cycle phase at encoding. Follicular women did not exhibit an emotional memory enhancement for gist ($F_{(1, 26)} = 2.8$, $p = 0.1$; see Fig 3b) or details ($F_{(1, 26)} = 1.4$, $p > 0.1$; see Fig 3b).

In contrast, luteal women exhibited no enhanced memory for gist in the emotional compared to the neutral condition, but showed a significant enhancement of memory for details ($F_{(1, 29)} = 5.13$, $p < .05$; see Fig 3c) from the emotional ($M = 8.0$, $SD = 4.2$) compared to the neutral ($M = 5.1$, $SD = 2.9$) condition.

3.2.3 Recall of Gist and Detail by Story Phase—We next examined which story phase was driving the overall enhancements for emotional gist memory in men and follicular women, and emotional detail memory in luteal women. First, we assessed gist and detail memory using separate 3 × 3 × 2 ANOVAs with menstrual phase at encoding, story phase (1 v. 2 v. 3), and emotional story content as independent factors. For gist memory, the 3 × 3 × 2 ANOVA revealed significant main effects of story phase ($F_{(2, 311)} = 18.1$, $p < .0001$) and emotional story content ($F_{(1, 312)} = 13.6$, $p < .001$) and a significant interaction effect of story phase × emotional story content ($F_{(2, 311)} = 3.95$, $p < .05$). No other main effects or interactions were significant. For detail memory, the 3 × 3 × 2 ANOVA revealed significant main effects of story phase ($F_{(2, 311)} = 33.1$, $p < .0001$) and emotional story content ($F_{(1, 312)} = 9.9$, $p < .01$). No other main effects or interactions were significant.

To investigate gist and detail memory in the different phases, we next assessed gist and detail memory in each phase of the story using a series of 3 × 2 ANOVAs with menstrual phase at encoding and emotional story content as independent factors. For phases 1 and 3, there were no main effects of emotional story content or menstrual phase at encoding, nor an interaction effect between these factors, on memory for gist or detail. For phase 2 however, we observed a main effect of emotion on gist recall ($F_{(1, 96)} = 12.7$, $p < .001$) and detail recall ($F_{(1, 96)} = 7.7$, $p < .01$). However, no main effects of menstrual phase at encoding or interaction effects were observed in the 3 × 2 ANOVAs for phase 2 gist and detail memory.

For men, enhanced recall of gist was driven by recall in phase 1 ($F_{(1, 37)} = 4.63$, $p < .05$) and phase 2 ($F_{(1, 37)} = 9.86$, $p < .01$) (Fig 5a). There were no recall differences observed for gist in phase 3, nor was there any difference in recall of story details observed for men in any story phase (Fig 4a). In follicular women, there was no enhanced recall of gist or detail in any phase, regardless of story condition (Fig 4b, 5b).

In luteal women, however, we observed different patterns of recall than those observed in men and follicular women. For luteal women, enhanced recall of details was driven by phase 2 ($F_{(1, 29)} = 6.8$, $p < .05$; see Fig 4c). No significant recall differences for story details were observed in phases 1 or 3. Luteal women did exhibit enhanced recall for story gist in phase 2 ($F_{(1, 29)} = 4.1$, $p = .05$; Fig 5c) of the emotional compared to the neutral story; no other gist recall differences were observed in phases 1 or 3.

3.2.4. Sex Hormone Levels and Recall of Gist and Detail—To explore potential relationships between sex hormone levels at encoding and emotional memory for gist and detail, we ran a series of correlations between these measures in luteal women, follicular women, and men. Luteal women demonstrated relationships between sex hormone levels at encoding and emotional memory for detail. In luteal women, correlations between sex

hormones at encoding and emotional detail memory revealed a significant positive relationship between testosterone and phase 2 detail memory ($r(14) = 0.62$, $p < .01$) as well as testosterone and total detail memory ($r(14) = 0.51$, $p < .05$). These two measures of emotional detail memory did not correlate with progesterone or 17β-estradiol in luteal women. Additionally in luteal women, phase 2 gist memory and total gist memory from the emotional story did not correlate with any of the sex hormones.

There were no significant correlations between testosterone and emotional gist or detail memory in men and follicular women.

3.3 Attention and Arousal

As an index of attention, we determined the average fixation time percentage for the four slides within phase 2, the most emotional phase of the emotional story. Men, follicular women, and luteal women all spent equivalent percentages of time fixated on the slides in phase 2 of the emotional story ($F_{(2, 47)} = 1.03$, $p > 0.1$; see Fig 6a). In addition to assessing attention in phase 2, we also examined whether participants explored the slides similarly in the emotional story as indicated by the number of glances and subsequently, fixation time percentage, made in the specified AOIs (Poole and Ball, 2005; Nielsen et al., 2011). There were no significant differences between men, follicular, and luteal women on either measure in any of the AOIs selected (data not shown).

Pupil diameter changes indicated arousal to the emotional component (phase 2) of the emotional story (Koss, 1986; Rajkowski, Kubiak, and Aston-Jones, 1993; Aston-Jones and Cohen, 2005; Nielsen et al., 2011). Men, follicular, and luteal women all exhibited equivalent average pupil diameter changes in response to phase 2 of the emotional story ($F_{(2, 46)} = 2.67$, $p > .05$; see Fig 6b). Additionally, no differences in average pupil dilation were observed in phase 1. However, in phase 3, there was a significant difference observed in pupil dilation between the three groups ($F_{(2, 46)} = 3.5$, $p < 0.05$). Post-hoc, a test for Tukey-Kramer HSD revealed that follicular women had greater pupil dilation ($M = 1.2 \pm 0.15$) compared to men ($M = 0.72 \pm 0.12$) ($p < .05$), but not luteal women ($M = 0.95 \pm 0.14$).

4. Discussion

The present findings are the first to demonstrate an influence of menstrual cycle phase at encoding on emotional memory for gist and detail, and they further support the view that both sex and menstrual cycle phase at encoding influence memory for an emotional experience. The influence was evident not in overall recall of the emotional story, but in the pattern of recall of story gist versus detail. Specifically, men exhibited enhanced memory for gist, but not details, from an emotional as compared to a neutral story, consistent with previous work using this emotional story paradigm (Cahill and van Stegeren, 2003). However, in naturally cycling women, memory for the emotional story varied with menstrual cycle phase at encoding. Memory for details from the emotional as compared to neutral story was only enhanced in women in the luteal (high sex hormone) phase of the menstrual cycle. Women in the follicular (low sex hormone) phase of the menstrual cycle did not exhibit a memory enhancement for emotional details or gist.

The present study is the first to explore the influence of menstrual cycle phase at encoding on retention of gist versus detail from an emotional experience. Recently, we demonstrated that hormonal contraception use altered retention of gist and detail from the same emotional story used here (Nielsen et al., 2011). We hypothesized that since hormonal contraception reduces endogenous levels of estrogen, progesterone, and testosterone (Rapkin, Morgan, Sogliano, Biggio, and Concas, 2006), it likely disrupted sex/stress hormone interactions

shown to influence emotional memory (Andreano and Cahill, 2010; van Wingen et al., 2008). Results from the present study are consistent with the possibility that sex/stress hormone interactions alter retention of gist and detail. Enhanced memory for details of the emotional story was only observed in naturally cycling women in the luteal (high hormone) phase of the menstrual cycle. Follicular (low hormone) women exhibited no emotional memory enhancement for details, which is consistent with previous work demonstrating that women with low endogenous sex hormones do not exhibit enhanced memory for emotional details (Nielsen et al., 2011). These results suggest that endogenous sex hormone levels at encoding influence memory for gist and detail from an emotional experience in women. More generally, but importantly, they strengthen the argument that failure to account for sex, menstrual cycle position, or hormonal contraceptive status at encoding can lead to inaccurate conclusions about the influence of emotional arousal on recall of gist and detail.

A possible explanation for the present findings is that a sex-related hemisphere laterality of amygdala function is modulated by sex hormones, and this may be driving differential retention of emotional gist and detail in men and women. The present study was not designed to specifically address the issue of potential amygdala involvement. However, results from the present study support previous findings that found β-adrenergic receptor blockers differentially impair emotional gist and detail memory in men and women (Cahill and van Stegeren, 2003). The present study also showed that sex hormone levels at encoding correlate with long-term emotional gist and detail memory in luteal women, respectively; suggesting that sex hormones modulate the consolidation of emotional information. Since the amygdala is critical for modulating the consolidation of emotional memories (McGaugh, 2000) and there is a sex-related hemispheric laterality of amygdala function (Cahill et al., 2004) and activity under resting state conditions (Kilpatrick et al., 2006), sex hormones at encoding may in fact modulate lateralized amygdala activity and its relationship with memory in men and women. However, these possibilities would have to be directly tested in future studies employing brain imaging methods.

The goal of this study was to better understand the influence(s) of sex and menstrual cycle position at encoding on retention of an emotional event. Although the results indicate that these factors play a role in emotional memory modulation of gist and detail, they raise several questions that should be further explored in future work. For example, correlation analyses revealed that in luteal women, testosterone positively correlated for phase 2 and overall detail memory from the emotional story. These observed relationships between sex hormones and memory for emotional gist and detail were not in line with our original predictions. However, they do raise the possibility that testosterone might modulate emotional detail memory in women when endogenous levels of progesterone and 17β-estradiol are high. While little is known about the relationship between testosterone and emotional memory, studies have shown that testosterone modulates amygdala activity in women (van Wingen et al., 2009); consequently, it may modulate some facet of emotional memory.

Considering these correlations more broadly, however, the analyses correspond with what we generally predicted. Sex hormone levels at encoding positively correlated only with emotional detail memory in luteal women. Clearly, however, before making absolute conclusions, it is imperative that these preliminary findings are confirmed in future investigations of emotional gist and detail memory.

Another point to consider is that in men, we observed that emotional memory for gist was enhanced in both story phases 1 and 2. Since story phase 1 is identical in both the emotional and neutral stories, and is relatively non-emotional, there may be a retrograde effect on phase 1 gist memory resulting from phase 2 arousal. Similar retrograde effects have been

reported in other emotional memory paradigms (Anderson et al., 2006; Strange and Dolan, 2004). A similar retention pattern was observed in hormonal contraception users (Nielsen et al., 2011). This retrograde effect may have been missed by earlier investigators using the 3-phase story method since no previous study addressed both sex and menstrual cycle effects at encoding. Thus further exploration is warranted to better understand the reasons for memory enhancement for phase 1 gist in some groups with this paradigm.

We also observed that, in follicular women, pupil dilation was enhanced for phase 3 of the emotional version of the story. The pupil dilation data suggested that follicular women were somewhat more aroused in phase 3 compared to men, although it is unclear as to why the follicular women may have been more aroused in phase 3 as compared to the other two groups. Thus, future work should explore potential causes of the enhanced arousal in phase 3 in follicular women, and potential implications for memory.

A final aspect of the present findings that warrants further exploration is the emotional memory enhancement of phase 2 gist in luteal women. On the basis of the hypothesis that the left hemisphere amygdala drives storage of detail memory in women (Cahill and van Stegeren, 2003) we predicted, and found, enhanced memory for story details in luteal women. However, we had not predicted that gist memory in the most emotional phase of the story would also be enhanced in luteal women. At present, it is unclear why luteal women recalled phase 2 gist better in the emotional compared to the neutral story. It is also unknown at present whether this effect is an anomaly, or perhaps a genuine reflection of sex hormones at encoding differentially influencing gist memory in the most emotionally arousing story phase. Thus we suggest that this too is an important direction for future studies of sex influences on memory using the emotional story paradigm.

Although our study was designed to explore the influence of sex and menstrual cycle phase at encoding on the consolidation of emotional memory, there is the possibility that there may be effects of sex hormones at retrieval. Future evidence of sex hormone or menstrual effects on retrieval would not change the main conclusion from our study, that they exert an effect at encoding; only that the encoding effects interact with retrieval effects to influence memory. Thus, future studies should investigate potential sex hormone influences at retrieval on the recall of emotional gist and detail in men and naturally cycling women.

There is also the possibility that memory for gist may be enhanced at different phases of the menstrual cycle that were not explored in this study. Although the range used here to classify “follicular” and “luteal” phases of the cycle is quite common (Azziz et al., 1999; Franklin et al., 2008; Sakaki and Mather, 2012; De Bondt et al., 2013), future studies may want to further explore the effects of menstrual phase at encoding on gist and detail memory by testing women in more specific phases. For example, future work could explore emotional gist and detail memory in women in the menses, early follicular, and late follicular stages of the menstrual cycle. Exploring emotional memory for gist and detail in these groups may reveal that emotional gist memory is enhanced in these different parts of the cycle.

The present findings may have important implications for understanding disorders of emotional memory that disproportionately affect women, such as clinical depression, anxiety disorders, and PTSD (Breslau, Davis, Andreski, and Peterson, 1991; Breslau, Davis, Andreski, Peterson, and Schultz, 1997; Kessler, Sonnega, Bromet, Hughes, and Nelson, 1995). These disorders have been shown to be related to learning and memory systems. Previous research, as well as our current study, clearly demonstrates that sex and sex hormones at encoding can influence these systems and modulation of emotional memory. Recent work with an experimental model of PTSD also showed that sex hormone levels at

the time of trauma may be critical in naturally cycling women (Soni, Curran, and Kamboj, 2013). Results from the study indicated a period of psychological vulnerability immediately following ovulation in women, and intrusion frequency was negatively correlated with the estrogen: progesterone ratio (Soni, Curran and Kamboj, 2013). Women in the early luteal phase (immediately post-ovulation) also showed higher rates of intrusive images, suggesting that intrusion frequency is modulated by sex hormone levels and menstrual cycle position in naturally cycling women.

In the clinical population, sex hormone influences on intrusions have also been identified. A recent study from our lab (Ferree et al., 2012) demonstrated that female rape victims experienced fewer intrusive symptoms if they were currently on hormonal contraception or had taken emergency contraception immediately after the sexual assault. In addition, women who took Ogestrel, a particular brand of emergency contraception, reported significantly lower post-traumatic stress total symptom levels than women that had taken a hormonally distinct emergency contraceptive, Plan B (Ferree et al., 2012), suggesting that sex hormone levels influence memory consolidation in the post-trauma period, thereby altering the likelihood of developing PTSD.

Although our current study did not explicitly examine disorders of emotional memory, the findings suggest that men and women differentially recall information from an emotional event. Our findings also demonstrate that in women, information recalled from an emotional event can vary depending on menstrual cycle phase at the time of the event. These findings, along with those from Nielsen et al. (2011), suggest that sex, sex hormones, and contraceptive status at encoding may modulate memory for emotional events. Thus, further investigation of how these factors influence memory for emotional events appears warranted for a full understanding of disorders related to emotional memory.

Acknowledgments

This work was supported by NIMH 575082 to LC.

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Highlights

- We examine effects of sex and menstrual phase on memory for an emotional story
- Men recall more gist items from an emotional story>Luteal women recall more detail items from an emotional story
- These groups don't differ on measures of attention or arousal during the story
- Sex and menstrual phase at encoding alters memory for an emotional event

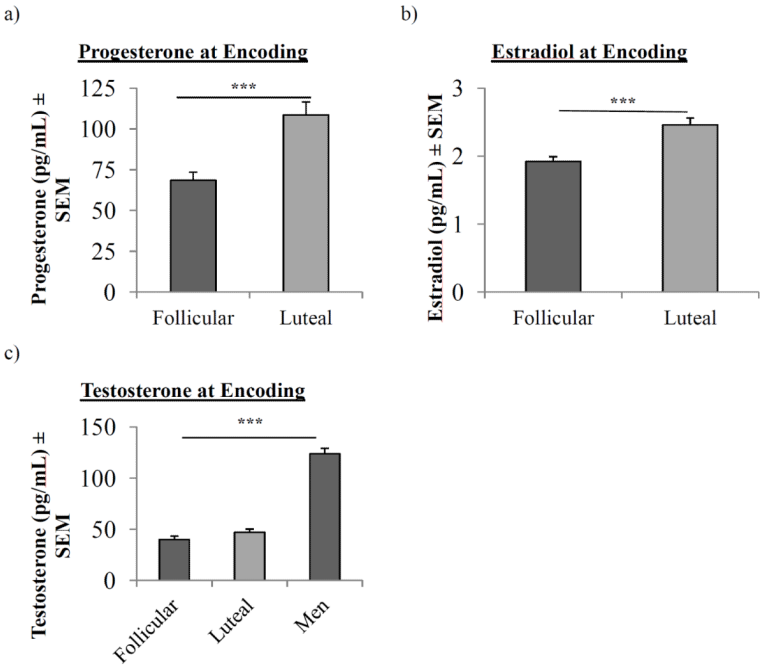

Fig. 1.

Sex steroid hormone levels in follicular women, luteal women, and men. **a,** Luteal women (*n* = 31) had significantly higher levels of progesterone than follicular women (*n* = 28; three asterisks, *P* < .0001). **b,** Luteal women (*n* = 31) had significantly higher levels of 17β-estradiol than follicular women (*n* = 28; three asterisks, *P* < .0001). **c,** Men (*n* = 39) had significantly higher levels of testosterone than follicular (*n* = 28) and luteal women (*n* = 31) (three asterisks, *P* < .0001). Values are means ± s.e.m.

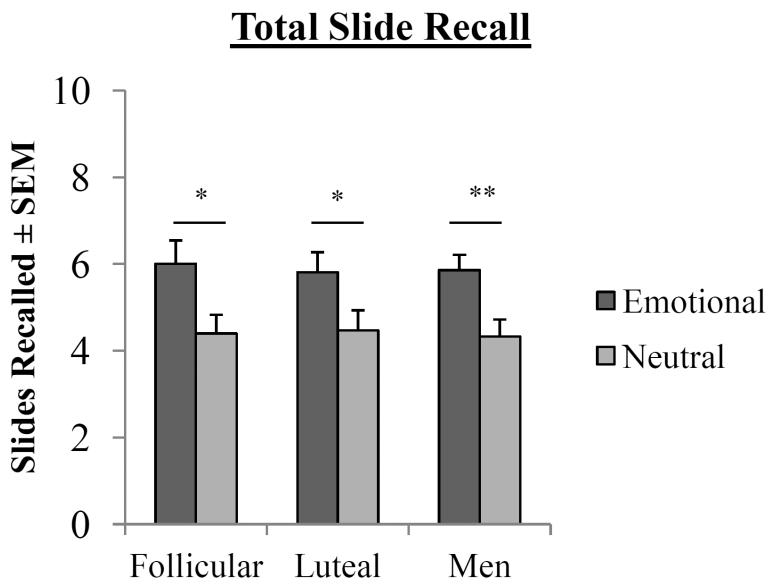

Fig. 2.

Total slide recall in follicular women, luteal women, and men. A 2 × 3 ANOVA revealed a main effect of emotion on total slide recall in follicular women, luteal women, and men (n = 28 follicular women, n = 31 luteal women, n = 39 men; one asterisk, $P < .05$, two asterisks, $P < .01$). Values are means ± s.e.m.

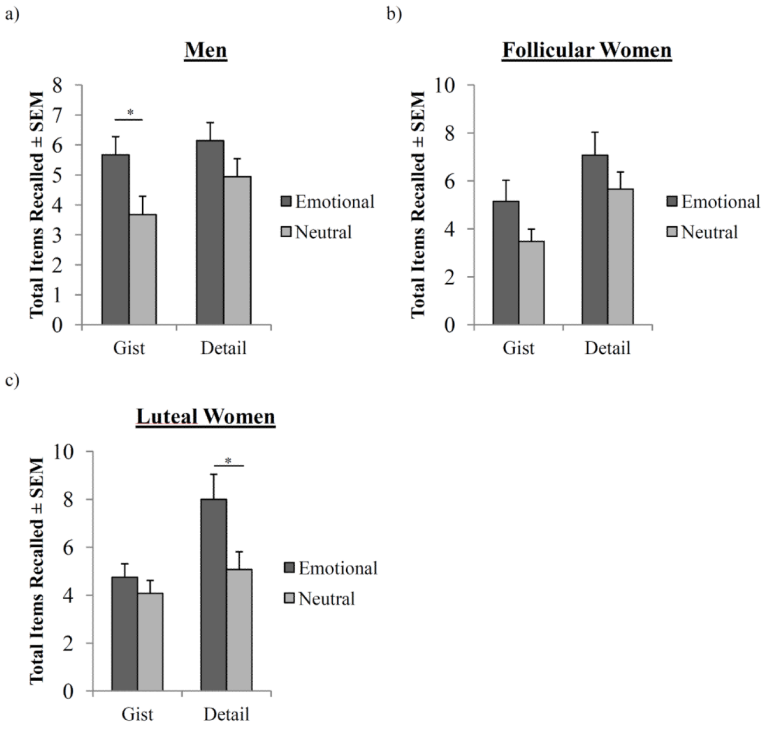

Fig. 3.

Total gist and detail item recall in men, follicular women, and luteal women. **a,** Men exhibited an effect of emotion for gist retention but not for details ($n = 39$; one asterisk, $P < .05$, one-way ANOVA). **b,** Follicular women exhibited no effect of emotion for gist retention or details ($n = 28$, one-way ANOVA). **c,** Luteal women exhibited an effect of emotion for detail retention but not for gist ($n = 31$; one asterisk, $P < .05$, one-way ANOVA). Values are means ± s.e.m.

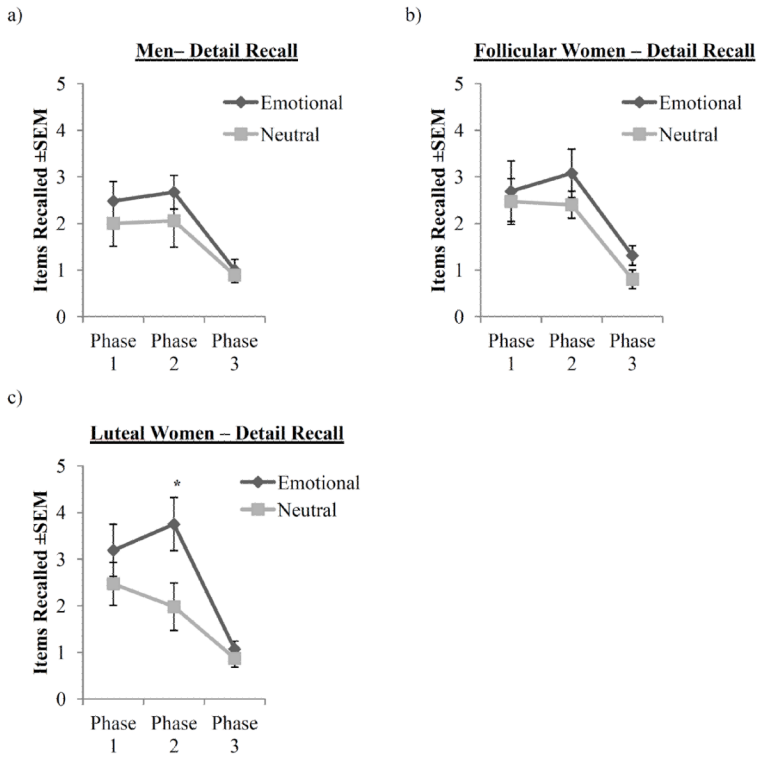

Fig. 4.

Recall of detail items by story phase in men, follicular women, and luteal women. **a,** Men (*n* = 39) exhibited no effect of emotion on detail retention in any story phase. **b,** Follicular women (*n* = 28) did not exhibit an effect of emotion on detail retention, regardless of story phase. **c,** Luteal women (*n* = 31) exhibited an effect of emotion on detail retention in Phase 2 (one asterisk, $P < .05$, one-way ANOVA). Values are means ± s.e.m.

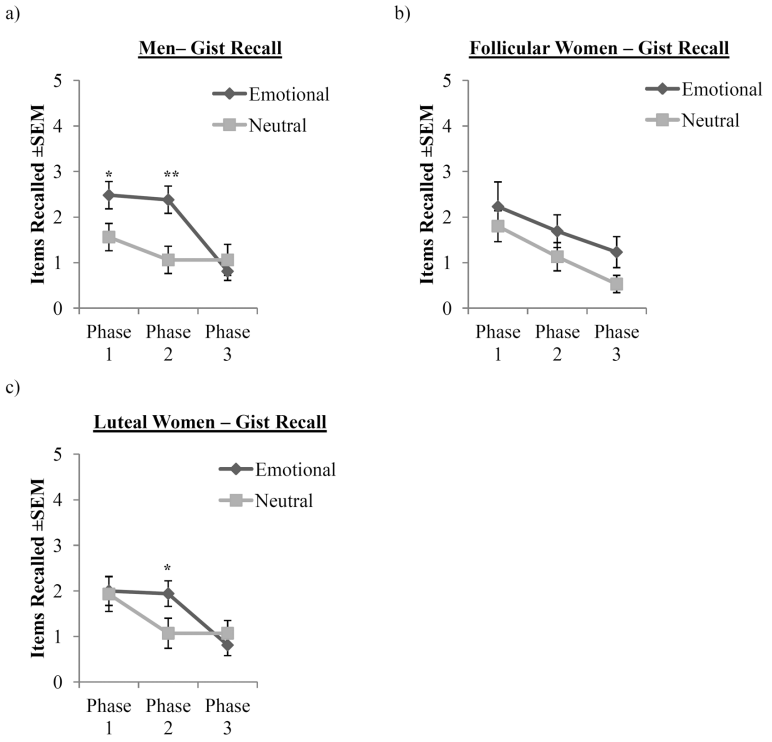

Fig. 5.

Recall of gist items by story phase in men, follicular women, and luteal women. **a,** Men (n = 39) exhibited an effect of emotion on gist retention in Phases 1 and 2 (two asterisks, $P < .01$; one asterisk, $P<.05$, one-way ANOVA, respectively). **b,** Follicular women (n = 28) exhibited no effect of emotion on gist retention in any phase (one-way ANOVA). **c,** Luteal women (n = 31) exhibited an effect of emotion on gist retention in Phase 2 (one asterisk, P = .05, one-way ANOVA). Values are means ± s.e.m.

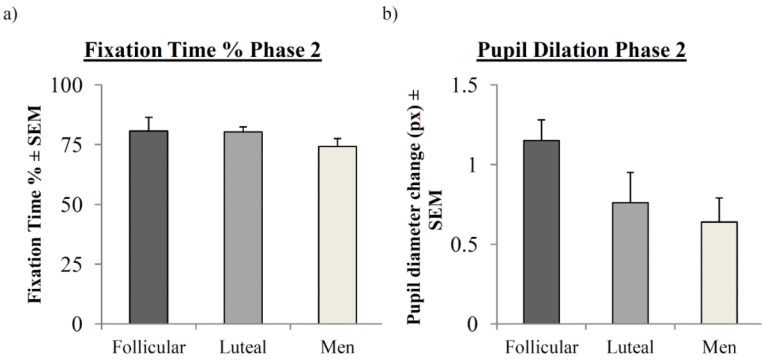

Fig. 6.

Attention and arousal in Phase 2 of the emotional story. **a,** No significant differences in average fixation time between follicular women, luteal women, and men (n = 13, n = 16, and n = 21, respectively). Values ± s.e.m. **b,** No significant differences in pupil dilation change between follicular women, luteal women, and men (n = 13, n = 16, and n = 20, respectively). Values ± s.e.m.

Table 1

Mean scores (± SEM) on cognitive measurements for Follicular, Luteal, and Men.

	Positive Affect (PA)*	Negative Affect (NA)	BEM***	Mehr**
Follicular	25.5 ± 1.6	13.8 ± .71	52.5 ± 1.9	10.9 ± 2.3
Luteal	27.4 ±1.3	15.1 ± 1.2	56.6 ± 1.5	16.0 ± 2.3
Men	30.0 ± 1.9	14.7 ± .84	48.0 ± 1.3	7.31 ± 2.3

* $p < .05$;

** $p < .01$;

*** $p < .001$