Effects of the Menstrual Cycle on Episodic Memory

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Date: 2021-11-13T00:00:00+00:00

Abstract

Theories and research findings from evolutionary psychology suggest that female sex hormones may be important factors influencing episodic memory, but the specific mechanisms remain unclear. This study takes the two phases constituted by natural changes in sex hormone levels during the female menstrual cycle (late follicular phase, mid-luteal phase) as independent variables, uses the "What-Where-When Task"episodic memory task (Experiment 1), combined with event-related potential (ERP) technology (Experiment 2), to investigate performance on episodic memory tasks and their possible underlying mechanisms across different menstrual cycle phases. Experiment 1 recruited 33 women with stable menstrual cycles as participants, who each participated in one session during the late follicular phase and one during the mid-luteal phase, completing in random order the O task (object memory only), P task (position memory only), OO task (object and its presentation order), OP task (object and its position), and PO task (position and order of object presentation). Results showed that when completing the PO task, recall accuracy during the mid-luteal phase was significantly higher than during the late follicular phase. Experiment 2 utilized event-related potential technology to further explore the reasons why the menstrual cycle affects episodic memory PO task performance, finding that the amplitude of P300 and LPC waves in frontal brain regions during the mid-luteal phase was significantly greater than during the late follicular phase, and that sensitivity during PO task completion was significantly positively correlated with right frontal P300 amplitude. Based on the above ERP results, it can be concluded that the superior performance on the PO task during the mid-luteal phase may benefit from significantly enhanced cognitive control ability, an explanation consistent with previous research findings. In summary, this study found that the menstrual cycle has a significant impact on memory for the integration of spatial position and temporal order of objects in episodic memory, with memory performance during the mid-luteal phase being significantly better than during the late follicular phase, possibly due to significantly enhanced

cognitive control ability during this phase. This study is expected to provide a new perspective for understanding factors influencing episodic memory.

Full Text

An Effect of Menstrual Cycle Phase on Episodic Memory

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Abstract

Evolutionary psychology theory and empirical findings suggest that female sex hormones may be important factors influencing episodic memory, but the specific mechanisms remain unclear. The present study used the natural hormonal fluctuations across the menstrual cycle to examine how two distinct cycle phases —the late follicular phase and mid-luteal phase—affect performance on episodic memory tasks and the underlying neural mechanisms. In Experiment 1, 33 women with stable menstrual cycles completed a "What-Where-When Task" during both cycle phases. The task included five conditions: object-only (O), position-only (P), object + order (OO), object + position (OP), and position + order (PO). Results showed that recall accuracy in the PO condition was significantly higher during the mid-luteal phase compared to the late follicular phase. Experiment 2 employed event-related potential (ERP) technology to investigate the neural basis of this effect. ERP results revealed significantly larger P300 and late positive component (LPC) amplitudes in frontal brain regions during the mid-luteal phase, and sensitivity during the PO task was significantly positively correlated with right frontal P300 amplitude. Based on these ERP findings, we propose that enhanced memory performance during the mid-luteal phase likely reflects strengthened cognitive control processes, consistent with previous research. In summary, this study demonstrates that menstrual cycle phase significantly affects the integration of spatial location and temporal order information in episodic memory, with superior performance during the mid-luteal phase potentially attributable to enhanced cognitive control. These findings provide a novel perspective on factors influencing episodic memory.

Keywords: Episodic Memory, Menstrual Cycle, Cognitive Control, P300, LPC, Event-Related Potential

Received: March 14, 2021
Funded by: National Natural Science Foundation of China (71971084)

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Introduction

In the 1970s, Tulving distinguished episodic memory from semantic memory, defining episodic memory as a system that stores information about *when*, *where*, and *what* happened—representing the conscious ability to remember the time and place of personally experienced events (Tulving, 2002). For example, during an exam, we might recall "I learned this material on a rainy day while sitting in a particular seat in the classroom," which facilitates retrieval. Thus, temporal and spatial context information associated with events can enhance our ability to retrieve past experiences. Episodic memory comprises two components: memory for object information and memory for contextual information. Object information refers to what the observer directly attends to (e.g., what the object is), while contextual information specifies the conditions under which the object was presented, including spatial location and temporal order (Chalfonte & Johnson, 1996). Episodic memory is a crucial component of human cognition, involving not only memory for objects and their spatiotemporal contexts but also the integration of these information types (Dere et al., 2006).

Recent research from evolutionary psychology and cognitive neuroscience suggests that the menstrual cycle may influence episodic memory. Specifically, female sex hormones exhibit not only lifelong changes (from low levels in childhood to peak levels in young adulthood and declining levels in old age) but also monthly cyclical fluctuations—the menstrual cycle—characterized by periodic changes in estrogen and progesterone levels (Sun et al., 2013). The typical menstrual cycle lasts 25–35 days (average 28 days) and can be divided into three phases: menstruation (days 1–6), follicular phase (days 7–14), and luteal phase (days 15–28) (Wilcox et al., 2000). During menstruation, both estrogen and progesterone are at their lowest levels. In the follicular phase, estrogen gradually increases, peaking one day before ovulation. In the luteal phase, progesterone rises progressively, reaching its peak in the mid-luteal phase (Ball et al., 2013).

From an evolutionary perspective, the menstrual cycle is functionally linked to reproductive and mating behaviors, with associated adaptive psychological and behavioral changes across cycle phases. For instance, during the luteal phase, women experience a pregnancy-like state that requires psychological adaptation to internal bodily changes and external social environments, as well as behavioral changes to protect the potential fetus and reduce risk-taking (Crawley et al., 2008). Empirical studies show that luteal-phase women, with elevated progesterone levels, become more sensitive to social support and threat cues, promoting self-protection (Barrett & Kurzban, 2006). Compared to the follicular phase, luteal-phase women show higher accuracy in recognizing fearful, angry, disgusted, and sad faces (Maner & Miller, 2014) and exhibit more frequent unconscious automatic recall of negative scenes, which positively corre-

lates with salivary progesterone levels (Ferree et al., 2011). Ertman et al. (2011) had women view neutral and negative images during ovulation and the luteal phase, then tested free recall one week later, finding better encoding of emotional images during the luteal phase, with salivary progesterone levels positively correlating with recall of emotional images. Luteal-phase women also show increased attention to social stimuli (Ackerman et al., 2009; Anderson et al., 2010; Reynolds et al., 2018) and display more prosocial behaviors (Stenstrom et al., 2018). In one study, women completed daily questionnaires for 35 days (covering an entire menstrual cycle), imagining how much money they would spend on relatives while shopping. Results showed that luteal-phase women allocated more money to relatives compared to the follicular phase. A subsequent study on anonymous donations to strangers similarly found more prosocial behavior during the luteal phase (Stenstrom et al., 2018).

Conversely, the primary goal during the late follicular phase is to seek high-quality potential mates. Research has found that women in the late follicular phase show faster recognition, better memory, and longer gaze duration for male faces, particularly masculine ones (Allan et al., 2012). Women also engage in more self-adornment behaviors during this phase (Zhuang & Wang, 2015) and walk with a more attractive gait in the presence of men (Guéguen, 2012; Miller et al., 2007), all aimed at attracting quality mates.

Some researchers propose that luteal-phase women mobilize cognitive control resources to encode social stimuli, enhancing detection of social information and sensitivity to harmful or beneficial cues, thereby promoting adaptive responses (Maner & Miller, 2014). Cognitive neuroscience research provides evidence for enhanced cognitive control during the luteal phase. For example, resting-state fMRI studies show significantly increased activation in the dorsolateral prefrontal cortex during the mid-luteal phase compared to the late follicular phase (Zhuang et al., 2020). In intertemporal choice tasks, women in the mid-luteal phase show significantly lower discount rates (An, 2018), and functional connectivity between the dorsolateral prefrontal cortex and striatum (a reward-related region) during the late follicular phase negatively correlates with discount rates (Zhuang et al., 2020). Extensive evidence indicates that the dorsolateral prefrontal cortex plays a crucial role in cognitive control. The quality of signal communication between the dorsolateral prefrontal cortex and dorsal striatum can regulate cognitive control over impulsivity (Cieslik et al., 2013; Sheline et al., 2010). The neural pathway connecting the right caudate head and putamen with the dorsolateral prefrontal cortex is recognized as a cognitive control circuit (Rotge et al., 2008). Generally, patients with obsessive-compulsive disorder (Van Den Heuvel et al., 2005), Parkinson' s disease (Williams-Gray et al., 2007), and Huntington' s disease (Watkins et al., 2000) show altered functional connectivity between the prefrontal cortex and striatum, accompanied by deficits in executive function. Research on internet gaming addiction found that reduced functional connectivity between the right caudate and dorsolateral prefrontal cortex correlates with cognitive control deficits (Yuan et al., 2016). A study on female smokers using resting-state fMRI across menstrual cycle phases found

that, compared to the luteal phase, follicular-phase women showed weakened functional connectivity between cognitive control regions and reward-related regions, along with reduced cognitive control over smoking behavior (Wetherill et al., 2016).

Current research on menstrual cycles has primarily focused on evolutionarily relevant domains such as mating and social interaction, with fewer studies examining effects on general cognitive abilities like episodic memory. It remains unclear which cognitive functions are affected by cyclical hormonal changes and how these changes influence episodic memory performance. As noted above, if enhanced cognitive control during the luteal phase is task-independent (as suggested by resting-state studies), it should also affect episodic memory. Furthermore, successful episodic memory involves not only memory for objects and contextual information but also integration of these information types, which requires strong cognitive control (DuBrow & Davachi, 2016; Jenkins & Ranganath, 2010). Based on these considerations, the present study selected the late follicular phase (when estrogen is near peak and progesterone is low) and mid-luteal phase (when both estrogen and progesterone are elevated) to investigate menstrual cycle effects on episodic memory. We hypothesized that: (1) Compared to the late follicular phase, women in the mid-luteal phase would show significantly enhanced integration ability for episodic memory components; and (2) This enhanced integration ability during the mid-luteal phase would involve active participation of brain regions associated with cognitive control, specifically the prefrontal cortex. Two experiments were conducted to test these hypotheses. Experiment 1 used the What-Where-When Task to explore menstrual cycle effects on episodic memory components and their integration. Experiment 2 employed ERP technology to test Hypothesis 2.

Experiment 1

Women with stable menstrual cycles were recruited to participate once during the late follicular phase and once during the mid-luteal phase. Using the What-Where-When Task paradigm, we investigated how the menstrual cycle affects episodic memory components and their integration.

Participants

Sample size was estimated using G*Power software (Faul et al., 2007). Based on previous research examining menstrual cycle effects on cognitive function, effect sizes are typically medium or larger. For example, Ikarashi et al. (2020) reported an effect size of 0.510 for menstrual cycle effects on declarative memory, and Yamazaki and Tamura (2017) reported an effect size of 0.604 for emotional expression recognition tasks. Therefore, we set parameters for a medium effect size of 0.50, with statistical power of 1 -β = 0.80 and α = 0.05, yielding a required sample size of 34 for paired-samples t-tests. Through a campus recruitment platform, we screened 36 right-handed female participants with normal or corrected-to-normal vision, aged 18-25 years (M $\pm$ SD: 20.79 $\pm$ 2.12), with

stable menstrual cycles of 28–30 days and no use of hormonal medications or devices. Three participants were excluded because their menstrual cycles were not stable after the experiment.

We used the counting-back method (Blake et al., 2016; Fales et al., 2014) to determine the two testing sessions: late follicular phase (late FP; 15–17 days before the first day of the next menstrual period) and mid-luteal phase (mid-LP; 6–8 days before the first day of the next period). Participants completed the same episodic memory task during both phases. The order of testing was counterbalanced: 17 participants were tested first in the late follicular phase and then in the mid-luteal phase, while the remaining 16 participants were tested in the reverse order. All participants provided informed consent and received compensation upon completion.

Experimental Task

The experiment employed the What-Where-When Task paradigm (Kessels et al., 1999), consisting of five conditions: object-only (O task), position-only (P task), object + order (OO task), object + position (OP task), and position + order (PO task). The independent variable was menstrual cycle phase (late follicular vs. mid-luteal), and the dependent variable was recall accuracy during the test phase.

Materials

Stimuli for the episodic memory task were selected through pre-testing (see example in [Figure 1: see original paper]). The materials consisted of color images of common everyday objects (animals, plants, stationery, clothing, daily necessities, etc.) on white backgrounds. Thirty-eight additional participants (14 males, aged 18–22: M ± SD = 20.7 ± 1.6; 24 females, aged 18–26: M ± SD = 20.3 ± 2.7) rated the familiarity of these items using a 9-point Likert scale (1 = very unfamiliar, 9 = very familiar). Fifty-eight images with mean familiarity ratings above 7 were selected as experimental materials. Thirty-five images were randomly chosen as learning materials and divided into five sets of seven images each, with each set randomly assigned to one experimental condition. The remaining 23 images served as distractors during the test phase. The experiment was programmed using E-Prime 2.0 and run on a 14-inch Lenovo laptop with a screen resolution of 1366 × 768 pixels and a vertical refresh rate of 60 Hz. Stimuli were presented in a 5 × 5 grid at the center of the screen. Participants sat 40–50 cm from the screen, with each object subtending approximately 2.65° of visual angle horizontally and vertically.

Procedure

Participants first completed a demographic questionnaire and informed consent form, then performed the five experimental tasks in random order on the computer. Each task consisted of a learning phase and a test phase. Before the learn-

ing phase, instructions explained the test phase requirements. During learning, seven object images were sequentially presented for 3 s each at random locations within the 5 × 5 grid (see [Figure 2: see original paper]A). After presentation, participants pressed the spacebar to begin the test phase. The test phase had no time limit; participants entered object or position numbers based on their memory (numbers were displayed only during testing for response convenience). After completing one task, participants proceeded to the next task' s learning and test phases until all five tasks were completed. The same procedure was repeated during both menstrual cycle phases.

The specific requirements for each task were as follows:

1. **O Task (Object-only, What)**: Learning: Remember only the objects presented, ignoring their order and position. Test: A 5 × 6 grid displayed 30 object images simultaneously, including the 7 studied objects and 23 distractors. Participants selected the 7 studied objects regardless of presentation order.
2. **P Task (Position-only, Where)**: Learning: Remember only which grid positions contained objects, ignoring the objects themselves and their order. Test: A blank 5 × 5 grid was displayed. Participants identified the positions where objects had appeared, in any order.
3. **OO Task (Object + Order, What and When)**: Learning: Remember both the objects and their presentation order, ignoring position. Test: A 5 × 6 grid displayed 30 object images (7 studied, 23 distractors). Participants entered the numbers of the 7 studied objects in their exact presentation order.
4. **OP Task (Object + Position, What and Where)**: Learning: Remember which objects appeared and their positions, ignoring order. Test: As shown in [Figure 2: see original paper]B, a blank 5 × 5 grid with numbered positions appeared on the left, and target objects with numbers appeared on the right. Participants matched each object to its studied position by entering paired numbers, in random order.
5. **PO Task (Position + Order, Where and When)**: Learning: Remember which positions contained objects and the order in which these positions were occupied, ignoring the specific objects. Test: A blank 5 × 5 grid was displayed. Participants entered the position numbers in the exact order they were presented during learning.

Results

A paired-samples t-test on recall accuracy across the two testing sessions revealed no significant order effects for any condition (see), indicating no practice effects.

Paired-samples t-tests comparing recall accuracy between menstrual cycle

phases for each task (descriptive statistics in) showed no significant differences for the O, P, OO, and OP tasks: t(32) = -1.36, p = 0.184, 95% CI [-0.07, 0.01], dz = 0.236; t(32) = -0.38, p = 0.707, 95% CI [-0.14, 0.10], dz = 0.067; t(32) = -1.08, p = 0.286, 95% CI [-0.14, 0.04], dz = 0.190; and t(32) = -1.68, p = 0.102, 95% CI [-0.16, 0.02], dz = 0.293, respectively. However, for the PO task, recall accuracy was significantly higher in the mid-luteal phase than in the late follicular phase, t(32) = -4.31, p < 0.001, 95% CI [-0.38, -0.14], dz = 0.750 (see [Figure 3: see original paper]).

Discussion

The results showed no significant differences between the two testing sessions, ruling out order or practice effects. Paired-samples t-tests revealed that only the PO task (memory for position and order) showed significantly better performance during the mid-luteal phase compared to the late follicular phase; no significant differences were found for the other tasks.

Examining the characteristics of the five memory tasks reveals that the PO task requires integration of both temporal and spatial contextual information, whereas the other four tasks require memory for only one type of contextual information or binding of objects with only one contextual dimension. The PO task thus involves more abstract information integration. Previous research has shown that older adults, despite intact memory for object information, exhibit significantly impaired ability to integrate multiple types of information, particularly temporal and spatial integration (Chalfonte & Johnson, 1996). This suggests that the PO task demands more cognitive control resources than the other tasks (DuBrow & Davachi, 2016). Cognitive control refers to the ability to flexibly promote task-relevant information processing and behavior while inhibiting or ignoring task-irrelevant information, particularly under conditions of interference or conflict. It is a high-level cognitive function essential for attention, working memory, language processing, and decision-making (Botvinick et al., 1999). To further test the cognitive control hypothesis for enhanced PO task performance during the mid-luteal phase, Experiment 2 collected ERP data during PO task performance to provide neural evidence.

Event-related potentials consist of exogenous and endogenous components. Exogenous components depend primarily on stimulus characteristics; physical properties of external information trigger attentional shifts and orienting, manifested as differences in potentials including P1, N1, N2, and P2 waves. The N1 and P1 components are associated with selective attention, with amplitudes positively correlated with attentional allocation—greater attention produces larger amplitudes, reflecting attentional focus on specific objects (Jha, 2002; Luo & Parasuraman, 2001). Increased N2 and P2 amplitudes generally indicate higher stimulus complexity and reflect the cortex' s ability to receive, process, and transmit information (Folstein & Van Petten, 2008; Näätänen & Picton, 1986). Endogenous components arise from internal mental activities, with individuals allocating cognitive resources according to behavioral goals

and intentions. The representative component is the P300, which appears around 300 ms and serves as an index for evaluating high-level cognitive activities such as sensation, memory, selective attention, and thinking (Howe et al., 2014). This component reflects psychological processes related to complex cognitive activities in associative cortices (Twomey et al., 2015), with amplitude positively correlated with task difficulty and mental resources required (Kumar et al., 2009; Moser et al., 2009). Recent research suggests that the scalp distribution of P300 may represent different cognitive components: parietal P300 may reflect automatic allocation of attentional resources, whereas frontal P300 may reflect cognitive control functions (Daffner et al., 2011; Fabiani & Friedman, 1995; Fjell & Walhovd, 2001; Kida et al., 2012; Kok, 2001; Yamaguchi & Knight, 1991).

According to dual-process models of memory retrieval, successful episodic memory retrieval depends on two distinct processes: familiarity and recollection. Familiarity refers to automatic retrieval of previously encountered people or objects without recalling specific spatiotemporal details (Kutas & Federmeier, 2011), whereas recollection requires cognitive control to provide precise episodic information. ERP studies show that familiarity-based retrieval is an automatic process associated with the early frontal-central negative potential N400 (Kutas & Federmeier, 2011), while recollection is associated with the late positive component (LPC) (Ecker et al., 2007; Woodruff et al., 2006). The LPC is a positive wave appearing between 500–800 ms that is related to recall accuracy and typically appears in central-parietal or left parietal regions (Curran & Cleary, 2003; Liu & Guo, 2020). Recent studies show this wave appears broadly across brain regions during memory retrieval (Nardini & Leynes, 2020) and is associated with self-related episodic recall (Brezis et al., 2017; Coronel & Federmeier, 2016; Leynes & Mok, 2017). Pathological research shows that hippocampal lesions substantially reduce LPC, demonstrating its strong relationship with memory (Addante et al., 2012; Hoppstädter et al., 2015). Furthermore, when participants are required to recall more details or retrieve context information simultaneously, stronger cognitive control demands produce larger LPC signals (Küper & Zimmer, 2018; Leynes & Crawford, 2018; Wilding, 1999).

In summary, we hypothesized that superior performance on the PO task during the mid-luteal phase, compared to the late follicular phase, would be attributable to enhanced cognitive control. Consequently, we predicted that mid-luteal phase would show significantly increased amplitudes of frontal P300 and LPC components during PO task performance.

Experiment 2

Participants

Based on the effect size from Experiment 1 for the PO task (dz = 0.750), G*Power analysis indicated that a sample size of 16 would provide adequate power (1 -β = 0.80, α = 0.05) for paired-samples t-tests. We recruited 30 fe-

male participants with stable menstrual cycles through campus advertisements (age 18–22: M ± SD = 20.13 ± 1.04), all with normal or corrected-to-normal vision. Using the same counting-back method as Experiment 1, we identified each participant' s late follicular and mid-luteal phases for testing. Two participants who completed only one session were excluded, leaving 28 valid participants (13 tested first in mid-luteal phase, 15 tested first in late follicular phase; age 19–22: M ± SD = 20.14 ± 0.93). Of these, 16 participants agreed to wear EEG equipment, while 12 completed only the behavioral task. Thus, ERP analyses included 16 participants, while behavioral analyses included 28 participants.

Experimental Task

The task was adapted from the PO task in Experiment 1. Using signal detection theory, we calculated dependent measures of recall accuracy, sensitivity, and response bias. The independent variable was menstrual cycle phase (late follicular vs. mid-luteal), and dependent variables included recall accuracy, sensitivity (d), and decision criterion (β).

Signal detection theory' s primary indices—discriminability (d) and decision criterion (β)—reflect an individual' s perceptual abilities, attitudes, and response tendencies during task performance. Discriminability (d) represents sensitivity, reflecting information encoding, processing, and memory quality (Xu et al., 2014), while the decision criterion reflects motivational and attitudinal changes (Yang & Zhong, 1996). By applying signal detection theory, we could determine whether superior PO task performance during the mid-luteal phase resulted from enhanced cognitive ability (sensitivity) or from conscious changes in response strategy.

Procedure

Participants first completed demographic questionnaires and informed consent. Sixteen participants were fitted with EEG caps before completing the PO task on the computer. The task consisted of 8 blocks, each comprising a learning phase and a test phase. During learning (see [Figure 4: see original paper]A), seven object images were sequentially presented for 3 s each at random positions within a 5 × 5 grid. All images were drawn from the learning and distractor materials from Experiment 1. Instructions emphasized that participants should remember only which positions contained objects and the order in which these positions were occupied, ignoring the objects themselves. After presentation, the test phase began immediately.

During testing ([Figure 4: see original paper]B), two objects from the learning phase were presented simultaneously in a 5 × 5 grid, both in positions that had been occupied during learning. Participants judged whether the left position had been presented earlier than the right position, pressing the "F" key for "yes" and the "J" key for "no." There was no time limit, and the next trial began automatically 500–800 ms after the response. Seven position-order judgments

were made per block. Participants completed 8 blocks (56 total judgments). The same procedure was repeated during both menstrual cycle phases.

ERP Data Collection

EEG was recorded using a 64-channel system with a 10–20 system extended electrode cap at a sampling rate of 1000 Hz and bandpass filter of 0.05–30 Hz. The ground electrode was positioned at the midpoint between Fpz and Fz. Two additional electrodes monitored eye movements: one placed 1 cm lateral to the left eye recorded horizontal electrooculogram (HEOG), and another placed 1 cm below the right orbit recorded vertical electrooculogram (VEOG). Electrode impedance was maintained below 10 kΩ using conductive gel to ensure good scalp contact.

ERP Data Processing and Statistical Analysis

EEG data were processed offline using EEGLAB. Data were downsampled to 250 Hz and re-referenced to the average of all electrodes. Bad epochs were manually removed before applying 0.1 Hz high-pass and 30 Hz low-pass filters. Independent Component Analysis (ICA) was used to detect and correct ocular and other artifacts. Trials with amplitudes exceeding $±$75 V were excluded. The analysis epoch spanned 1000 ms post-stimulus, with a 200 ms pre-stimulus baseline. Latency and peak amplitude were used as metrics. ERP waveforms were averaged across participants and conditions using the ERPlab plugin.

Based on previous research, electrodes were grouped into nine regions of interest (ROIs): midline (Cz, Pz, CPz), left frontal (F1, F3, FC3), right frontal (F2, F4, FC4), left central (C1, C3, CP3), right central (C2, C4, CP4), left parietal (P1, P3, PO3), and right parietal (P2, P4, PO4) (see [Figure 5: see original paper]) (Ecker et al., 2007; Tanguay et al., 2018). Consistent with previous research and our hypotheses, we focused on two late components: P300 (260–320 ms) and LPC (480–670 ms) (Bermúdez-Margaretto et al., 2018; Ecker et al., 2007). Latency and amplitude for each component in each ROI were first compared between cycle phases using paired-samples t-tests, followed by repeated-measures ANOVA to examine main effects of menstrual cycle phase and ROI, as well as potential interactions.

Results

Behavioral Results Hits were defined as correct judgments matching the learning phase exactly, while false alarms were incorrect judgments of different presentations as identical. Sensitivity (d) and decision criterion (β) were calculated using signal detection theory, where d = Z(hit rate) -Z(false alarm rate) and β = O(hit rate)/O(false alarm rate). Hit and false alarm rates were converted to Z-scores (Yang & Zhong, 1996) to compute sensitivity and criterion for each participant in both phases.

Response accuracy, sensitivity, and decision criterion are shown in . Paired-samples t-tests revealed a significant difference in accuracy between cycle phases, t(27) = -2.15, p = 0.040, 95% CI [-6.90, -0.16], dz = 0.528, with higher accuracy in the mid-luteal phase, replicating Experiment 1 results. Sensitivity showed a marginally significant difference, t(27) = -1.94, p = 0.063, 95% CI [-0.78, 0.02], dz = 0.456, also favoring the mid-luteal phase. Decision criterion did not differ significantly between phases, t(27) = -0.87, p = 0.390, 95% CI [-2.22, 0.93], dz = 0.264.

ERP Results Average ERP waveforms for both cycle phases across ROIs are shown in [Figure 6: see original paper], with topographic maps in [Figure 7: see original paper].

P300 Component (260–320 ms). The P300 component appeared in all ROIs, with no significant latency differences between cycle phases (see [Figure 6: see original paper]). Amplitude comparisons revealed that right frontal P300 amplitude was significantly smaller in the late follicular phase (-3.47 ± 1.72 V) than in the mid-luteal phase (-2.68 ± 1.80 V), t(15) = 3.06, p = 0.008, 95% CI [-1.34, -0.24], dz = 0.824. Conversely, left parietal P300 amplitude was significantly larger in the late follicular phase (5.14 ± 2.70 V) than in the mid-luteal phase (4.25 ± 2.61 V), t(15) = 2.72, p = 0.016, 95% CI [0.19, 1.59], dz = 0.547. Similar patterns were observed at Pz (late follicular: 4.53 ± 2.75 V; mid-luteal: 3.58 ± 2.43 V), t(15) = 2.42, p = 0.029, 95% CI [0.11, 1.79], dz = 0.479, and right parietal sites (late follicular: 5.83 ± 2.85 V; mid-luteal: 4.74 ± 2.83 V), t(15) = 2.96, p = 0.010, 95% CI [0.30, 1.86], dz = 0.596.

A 2 (menstrual cycle phase: late follicular, mid-luteal) × 3 (anterior-posterior ROI: frontal, central, parietal) × 3 (lateral ROI: left, midline, right) repeated-measures ANOVA revealed a significant interaction between menstrual cycle phase and anterior-posterior ROI, F(2, 30) = 11.83, p < 0.001, p^2 = 0.441. Follow-up tests showed larger amplitudes in frontal regions during the mid-luteal phase (Mmid-luteal -Mlate-follicular = 0.52 V, p = 0.048) and larger amplitudes in parietal regions during the late follicular phase (Mmid-luteal -Mlate-follicular = -0.97 V, p = 0.008).

Late Positive Component (LPC). Paired-samples t-tests showed that right frontal LPC amplitude was significantly larger in the mid-luteal phase (-0.67 ± 1.00 V) than in the late follicular phase (-1.14 ± 1.09 V), t(15) = 2.59, p = 0.020, 95% CI [-0.86, -0.08], dz = 0.652. A 2 (menstrual cycle phase) × 3 (anterior-posterior ROI) × 3 (lateral ROI) repeated-measures ANOVA revealed no significant main effect of menstrual cycle phase or interactions with ROI.

Early ERP Component (N1). The N1 component appeared in left central, Cz, and CPz regions, with no significant latency differences between cycle phases across ROIs (see [Figure 6: see original paper]). Amplitude comparisons revealed that left central N1 amplitude was significantly larger in the late follicular phase (0.80 ± 0.77 V) than in the mid-luteal phase (0.33 ± 0.77 V), t(15)

= 3.09, p = 0.007, 95% CI [-0.78, -0.15], dz = 0.746. Similar patterns were observed at Cz (late follicular: 0.83 ± 1.49 V; mid-luteal: 0.36 ± 1.24 V), t(15) = 3.13, p = 0.007, 95% CI [-0.78, -0.15], dz = 0.748, and CPz (late follicular: 0.67 ± 1.15 V; mid-luteal: 0.10 ± 0.91 V), t(15) = 2.30, p = 0.036, 95% CI [-1.10, -0.04], dz = 0.620. A 2 × 3 × 3 repeated-measures ANOVA revealed only a marginally significant main effect of menstrual cycle phase, F(1, 15) = 4.39, p = 0.054, p^2 = 0.226, with larger amplitudes in the late follicular phase (0.42 ± 1.81 V) than in the mid-luteal phase (0.13 ± 1.95 V). No significant effects were found for other components.

Correlation Analysis Between Behavior and ERPs P300 Component. We correlated PO task accuracy and sensitivity with ERP data (average amplitude 260–320 ms) from right frontal, left parietal, right parietal, and Pz electrodes. Right frontal amplitude showed a significant positive correlation with sensitivity (r = 0.408, p = 0.025; see [Figure 8: see original paper]).

LPC Component. Correlations between PO task accuracy/sensitivity and ERP data (average amplitude 480–670 ms) from the right frontal region revealed no significant relationships (p > 0.4).

N1 Component. Correlations between PO task accuracy/sensitivity and ERP data from left central, Cz, and CPz electrodes (N1 amplitude) showed that CPz amplitude was significantly negatively correlated with both accuracy (r = -0.409, p = 0.025) and sensitivity (r = -0.381, p = 0.038; see [Figure 9: see original paper]).

Discussion

Behavioral data showed significantly higher recall accuracy during the mid-luteal phase than the late follicular phase. Sensitivity showed a marginally significant difference, also favoring the mid-luteal phase, while decision criterion did not differ between phases. ERP results revealed menstrual cycle differences in N1, P300, and LPC components during PO task performance. Specifically, the P300 showed a significant interaction between menstrual cycle phase and brain region: frontal regions showed larger amplitudes during the mid-luteal phase, while parietal regions showed larger amplitudes during the late follicular phase. For the LPC, right frontal amplitude was significantly larger during the mid-luteal phase. Previous research indicates that frontal, particularly right frontal, P300 and LPC amplitudes are strongly associated with cognitive control engagement (Fabiani & Friedman, 1995; Küper & Zimmer, 2018; Leynes & Crawford, 2018; Wilding, 1999; Fjell & Walhovd, 2001). These findings suggest that enhanced cognitive control contributes to improved PO task performance during the mid-luteal phase, consistent with previous fMRI research (Zhuang et al., 2020) showing stronger cognitive control during the mid-luteal phase in both resting-state and task-based paradigms. The positive correlation between sensitivity and right frontal P300 amplitude further supports our hypothesis

that memory improvements during the mid-luteal phase are due to enhanced cognitive control rather than changes in motivation or task attitude.

Conversely, N1 amplitude was significantly larger during the late follicular phase. Since N1 amplitude is positively correlated with selective attention, reflecting attentional allocation to specific objects and capture of attentional resources by external stimuli (Jha, 2002; Luo & Parasuraman, 2001), this suggests that the late follicular phase involves greater attentional resource allocation to memory objects. The larger parietal P300 amplitude during the late follicular phase further indicates greater automatic attentional engagement (Kida et al., 2012). The negative correlation between CPz N1 amplitude and both accuracy and sensitivity suggests that excessive attentional resource allocation to external stimuli during the late follicular phase may reduce cognitive control, leading to poorer performance.

In summary, these results indicate that during PO task performance, the mid-luteal phase involves stronger cognitive control that enhances memory performance, whereas the late follicular phase involves greater attentional resource allocation to external stimuli, which may impair performance.

General Discussion

Experiment 1 demonstrated that menstrual cycle phase affects the integration of spatial location and temporal order information (PO task) in episodic memory. Experiment 2, using ERP technology, revealed larger P300 and LPC amplitudes in frontal regions during the mid-luteal phase compared to the late follicular phase. These findings suggest that superior PO task performance during the mid-luteal phase benefits from enhanced cognitive control. In contrast, larger N1 and parietal P300 amplitudes during the late follicular phase indicate greater automatic attentional engagement with external stimuli. These results suggest that menstrual cycle effects on episodic memory may share underlying mechanisms with effects on reproductive and mating behaviors. Future research could simultaneously measure both types of tasks while precisely assessing hormonal levels and using neuroimaging techniques to identify how menstrual cycle-related hormonal changes alter brain structure and function.

The significance of this study lies in its examination of menstrual cycle effects on general cognitive ability (episodic memory) outside reproductive or mating contexts, demonstrating that these effects persist in neutral contexts. This suggests that cognitive abilities shaped by reproductive hormones may broadly influence behavior across social situations. For example, research using visual cue tasks has found that high progesterone levels increase general sensitivity to social stimuli, independent of specific social intentions (Maner & Miller, 2014). This aligns with our finding of better sensitivity during the mid-luteal phase independent of task motivation or attitude. Future studies should explore how menstrual cycle phases shape dopaminergic pathway structure and function and their relationship to specific social and cognitive tasks.

Furthermore, using the menstrual cycle to study hormonal effects on episodic memory offers greater ecological validity than focusing on single hormones, as both age-related and cycle-related hormonal changes involve coordinated fluctuations of multiple hormones. Research has shown that discount rates in intertemporal choice during the mid-luteal phase correlate positively with the ratio of estrogen to progesterone levels (Zhuang et al., 2020). Future studies should measure hormone levels across cycle phases to determine how specific or relative hormone levels relate to episodic memory performance, potentially providing insights into multi-hormone coordination in cognition and behavior.

Practically, these findings may inform interventions for hormone-related memory decline and contribute to understanding memory disorders such as Alzheimer' s disease. Previous research indicates that estrogen is involved in the pathophysiology of Alzheimer' s and Parkinson' s diseases and modulates dopamine-related cognitive processes (Arevalo et al., 2014; Li et al., 2014; Tuscher et al., 2016). Our results suggest that interventions should consider coordinated effects of multiple hormones.

This study has several limitations. First, without a baseline condition, we cannot determine whether enhanced cognitive control during the mid-luteal phase represents an absolute improvement or results from diminished cognitive control during the late follicular phase. Future research should include a control group. Second, without direct hormone measurements, we cannot identify which specific hormones or their relative levels drive the observed PO task performance differences. Future studies should incorporate hormonal assays.

Conclusion

Using the What-Where-When Task to investigate menstrual cycle effects on episodic memory, we found: (1) Menstrual cycle phase significantly affects memory for integrated spatial location and temporal order information, with superior performance during the mid-luteal phase compared to the late follicular phase. (2) Enhanced integration ability during the mid-luteal phase is associated with increased P300 and LPC amplitudes in frontal brain regions, likely reflecting strengthened cognitive control.

References

Ackerman, J. M., Becker, D. V., Mortensen, C. R., Sasaki, T., Neuberg, S. L., & Kenrick, D. T. (2009). A pox on the mind: Disjunction of attention and memory in the processing of physical disfigurement. *Journal of Experimental Social Psychology, 45*(3), 478–485.

Addante, R. J., Ranganath, C., Olichney, J., & Yonelinas, A. P. (2012). Neurophysiological evidence for a recollection impairment in amnesia patients that leaves familiarity intact. *Neuropsychologia, 50*(13), 3004–3014.

Allan, K., Jones, B. C., DeBruine, L. M., & Smith, D. S. (2012). Evidence of adaptation for mate choice within women' s memory. *Evolution and Human Behavior, 33*(3), 193–199.

Anderson, U. S., Perea, E. F., Becker, D. V., Ackerman, J. M., Shapiro, J. R., Neuberg, S. L., & Kenrick, D. T. (2010). I only have eyes for you: Ovulation redirects attention (but not memory) to attractive men. *Journal of Experimental Social Psychology, 46*(5), 804–808.

An, X. F. (2018). *An Experimental Study on the Effect of Menstrual Cycle on Intertemporal Choice and Interpersonal Choice* (Master' s thesis). East China Normal University. Available from CNKI. [安小芬. (2018). 生理周期影响跨期决策和跨人际决策的实验研究. (硕士). 华东师范大学, Available from Cnki.]

Arevalo, M. A., Azcoitia, I., & Garcia-Segura, L. M. (2014). The neuroprotective actions of oestradiol and oestrogen receptors. *Nature Reviews Neuroscience, 16*(1), 17–29.

Ball, A., Wolf, C. C., Ocklenburg, S., Herrmann, B. L., Pinnow, M., Brüne, M., ···& Güntürkün, O. (2013). Variability in ratings of trustworthiness across the menstrual cycle. *Biological Psychology, 93*(1), 52–57.

Barrett, H. C., & Kurzban, R. (2006). Modularity in Cognition: Framing the Debate. *Psychological Review, 113*(3), 628–647.

Bermúdez-Margaretto, B., Beltrán, D., Cuetos, F., & Domínguez, A. (2018). Brain Signatures of New (Pseudo-) Words: Visual Repetition in Associative and Non-associative Contexts. *Frontiers in Human Neuroscience, 12*(354).

Blake, K. R., Dixson, B. J. W., O' Dean, S. M., & Denson, T. F. (2016). Standardized protocols for characterizing women' s fertility: A data-driven approach. *Hormones and Behavior, 81*, 74–83.

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature, 402*(6758), 179–181.

Brezis, N., Bronfman, Z. Z., Yovel, G., & Goshen-Gottstein, Y. (2017). The Electrophysiological Signature of Remember–Know Is Confounded with Memory Strength and Cannot Be Interpreted as Evidence for Dual-process Theory of Recognition. *Journal of Cognitive Neuroscience, 29*(2), 334–345.

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory & Cognition, 24*(4), 403–416.

Cieslik, E. C., Zilles, K., Caspers, S., Roski, C., Kellermann, T. S., Jakobs, O., . . . Eickhoff, S. B. (2013). Is There "One" DLPFC in Cognitive Action Control? Evidence for Heterogeneity From Co-Activation-Based Parcellation. *Cerebral Cortex, 23*(11), 2677–2689.

Coronel, J. C., & Federmeier, K. D. (2016). The N400 reveals how personal semantics is processed: Insights into the nature and organization of self-knowledge.

Neuropsychologia, 84, 36–43.

Crawley, R., Grant, S., & Hinshaw, K. (2008). Cognitive Changes in Pregnancy: Mild Decline or Societal Stereotype? *Applied Cognitive Psychology, 22*(8), 1142–1162.

Curran, T., & Cleary, A. M. (2003). Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research, 15*(2), 191–205.

Daffner, K. R., Chong, H., Sun, X., Tarbi, E. C., Riis, J. L., McGinnis, S. M., & Holcomb, P. J. (2011). Mechanisms Underlying Age- and Performance-related Differences in Working Memory. *Journal of Cognitive Neuroscience, 23*(6), 1298–1314.

Dere, E., Kart-Teke, E., Huston, J. P., & Silva, M. D. S. (2006). The case for episodic memory in animals. *Neuroscience and Biobehavioral Reviews, 30*(8), 1206–1224.

DuBrow, S., & Davachi, L. (2016). Temporal binding within and across events. *Neurobiology of Learning and Memory, 134*, 107–114.

Ecker, U. K. H., Zimmer, H. D., & Groh-Bordin, C. (2007). Color and context: An ERP study on intrinsic and extrinsic feature binding in episodic memory. *Memory & Cognition, 35*(6), 1483–1501.

Ertman, N., Andreano, J. M., & Cahill, L. (2011). Progesterone at encoding predicts subsequent emotional memory. *Learning & Memory, 18*(12), 759–763.

Fabiani, M., & Friedman, D. (1995). Changes in brain activity patterns in aging: The novelty oddball. *Psychophysiology, 32*(6), 579–594.

Fales, M. R., Gildersleeve, K. A., & Haselton, M. G. (2014). Exposure to perceived male rivals raises men' s testosterone on fertile relative to nonfertile days of their partner' s ovulatory cycle. *Hormones and Behavior, 65*(5), 454–460.

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences.* Behavior Research Methods, 39*, 175–191.

Ferree, N. K., Kamat, R., & Cahill, L. (2011). Influences of menstrual cycle position and sex hormone levels on spontaneous intrusive recollections following emotional stimuli. *Consciousness and Cognition, 20*(4), 1154–1162.

Fjell, A. M., & Walhovd, K. B. (2001). P300 and neuropsychological tests as measures of aging: scalp topography and cognitive changes. *Brain Topography, 14*(1), 25–40.

Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology, 45*(1), 152–170.

Guéguen, N. (2012). Gait and menstrual cycle: Ovulating women use sexier gaits and walk slowly ahead of men. *Gait & Posture, 35*(4), 621–624.

Hoppstädter, M., Baeuchl, C., Diener, C., Flor, H., & Meyer, P. (2015). Simultaneous EEG–fMRI reveals brain networks underlying recognition memory ERP old/new effects. *NeuroImage, 116*, 163–173.

Howe, A. S., Bani-Fatemi, A., & De Luca, V. (2014). The clinical utility of the auditory P300 latency subcomponent event-related potential in preclinical diagnosis of patients with mild cognitive impairment and Alzheimer' s disease. *Brain and Cognition, 86*(1), 64–74.

Ikarashi, K., Sato, D., Iguchi, K., Baba, Y., & Yamashiro, K. (2020). Menstrual Cycle Modulates Motor Learning and Memory Consolidation in Humans. *Brain Sciences, 10*(10), 696.

Jenkins, L. J., & Ranganath, C. (2010). Prefrontal and Medial Temporal Lobe Activity at Encoding Predicts Temporal Context Memory. *Journal of Neuroscience, 30*(46), 15558–15565.

Jha, A. P. (2002). Tracking the time-course of attentional involvement in spatial working memory: an event-related potential investigation. *Cognitive Brain Research, 15*(1), 61–69.

Kessels, R. P. C., Postma, A., & de Haan, E. H. F. (1999). Object relocation: a program for setting up, running, and analyzing experiments on memory for object locations. *Behavior Research Methods, Instruments, & Computers, 31*(3), 423–428.

Kida, T., Kaneda, T., & Nishihira, Y. (2012). Dual-task repetition alters event-related brain potentials and task performance. *Clinical Neurophysiology, 123*(6), 1123–1130.

Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology, 38*(3), 557–577.

Kumar, S., Soto, D., & Humphreys, G. W. (2009). Electrophysiological evidence for attentional guidance by the contents of working memory. *European Journal of Neuroscience, 30*(2), 307–317.

Küper, K., & Zimmer, H. D. (2018). The impact of perceptual changes to studied items on ERP correlates of familiarity and recollection is subject to hemispheric asymmetries. *Brain and Cognition, 122*, 17–25.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology, 62*(1), 621–647.

Leynes, P. A., & Crawford, C. J. (2018). Event-related potential (ERP) evidence that encoding focus alters recollected features. *Brain and Cognition, 127*, 42–50.

Leynes, P. A., & Mok, B. A. (2017). Encoding focus alters diagnostic recollection and event-related potentials (ERPs). *Brain and Cognition, 117*, 1-11.

Li, R., Cui, J., & Shen, Y. (2014). Brain sex matters: Estrogen in cognition and Alzheimer' s disease. *Molecular and Cellular Endocrinology, 389*(1-2), 13-21.

Liu, Z., & Guo, C. (2020). Unitization could facilitate item recognition but inhibit verbatim recognition for picture stimuli: behavioral and event-related potential study. *Psychological Research, 85*(8), 3065-3079.

Luo, Y. J., & Parasuraman, R. (2001). The Early ERP Effects Reflect Neural Activity in Spatial Scale of Visual Attention. *Acta Psychologica Sinica, 33*(5), 385-389. [罗跃嘉 & Parasuraman, R. (2001). 早期 ERP 效应与视觉注意空间等级的脑调节机制. 心理学报 (05), 385-389.]

Maner, J. K., & Miller, S. L. (2014). Hormones and social monitoring: Menstrual cycle shifts in progesterone underlie women' s sensitivity to social information. *Evolution and Human Behavior, 35*(1), 9-16.

Miller, G., Tybur, J. M., & Jordan, B. D. (2007). Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evolution and Human Behavior, 28*(6), 375-381.

Moser, J. S., Krompinger, J. W., Dietz, J., & Simons, R. F. (2009). Electrophysiological correlates of decreasing and increasing emotional responses to unpleasant pictures. *Psychophysiology, 46*(1), 1-7.

Näätänen, R., & Picton, T. (1986). N2 and automatic versus controlled processes. *Electroencephalography & Clinical Neurophysiology Supplement, 38*, 169-186.

Nardini, C. L., & Leynes, P. A. (2020). Encoding focus does not affect recollection of action memories: Event related potential (ERP) and modeling evidence. *International Journal of Psychophysiology, 147*, 9-17.

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*(10), 2128-2148.

Reynolds, T. A., Makhanova, A., Marcinkowska, U. M., Jasienska, G., McNulty, J. K., Eckel, L. A., . . . Maner, J. K. (2018). Progesterone and women's anxiety across the menstrual cycle. *Hormones and Behavior, 102*, 34-40.

Rotge, J. Y., Guehl, D., Dilharreguy, B., Cuny, E., Tignol, J., Bioulac, B., ···& Aouizerate, B. (2008). Provocation of obsessive-compulsive symptoms: a quantitative voxel-based meta-analysis of functional neuroimaging studies. *Journal of psychiatry & neuroscience: JPN, 33*(5), 405-412.

Sheline, Y. I., Price, J. L., Yan, Z., & Mintun, M. A. (2010). Resting-state functional MRI in depression unmasks increased connectivity between networks via the dorsal nexus. *Proceedings of the National Academy of Sciences, 107*(24), 11020-11025.

Stenstrom, E. P., Saad, G., & Hingston, S. T. (2018). Menstrual cycle effects on prosocial orientation, gift giving, and charitable giving. *Journal of Business Research, 84*, 82-88.

Sun, X. L., Liu, Y. F., Sun, T. L., & Zhao, Y. (2013). Research Situation of the Women' s Menstrual Cycle Performance and Impact Factors. *China Medical Herald, 10*(18), 33-35+38. [孙晓丽, 刘雁峰, 孙天琳, & 赵燕. (2013). 女性月经周期相关表现及影响因素的研究概况. 中国医药导报, 10(18), 33-35+38.]

Tanguay, A. N., Benton, L., Romio, L., Sievers, C., Davidson, P. S. R., & Renoult, L. (2018). The ERP correlates of self-knowledge: Are assessments of one' s past, present, and future traits closer to semantic or episodic memory? *Neuropsychologia, 110*, 65-83.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology, 53*(1), 1-25.

Tuscher, J. J., Szinte, J. S., Starrett, J. R., Krentzel, A. A., Fortress, A. M., Remage-Healey, L., & Frick, K. M. (2016). Inhibition of local estrogen synthesis in the hippocampus impairs hippocampal memory consolidation in ovariectomized female mice. *Hormones and Behavior, 83*, 60-67.

Twomey, D. M., Murphy, P. R., Kelly, S. P., & O' Connell, R. G. (2015). The classic P300 encodes a build-to-threshold decision variable. *European Journal of Neuroscience, 42*(1), 1636-1643.

Van Den Heuvel, O. A., Veltman, D. J., Groenewegen, H. J., Cath, D. C., Van Balkom, A. J., Van Hartskamp, J., ···& Van Dyck, R. (2005). Frontal-striatal dysfunction during planning in obsessive-compulsive disorder. *Archives of general psychiatry, 62*(3), 301-309.

Watkins, L. H., Rogers, R. D., Lawrence, A. D., Sahakian, B. J., Rosser, A. E., & Robbins, T. W. (2000). Impaired planning but intact decision making in early Huntington' s disease: implications for specific fronto-striatal pathology. *Neuropsychologia, 38*(8), 1112-1125.

Wetherill, R. R., Jagannathan, K., Hager, N., Maron, M., & Franklin, T. R. (2016). Influence of menstrual cycle phase on resting-state functional connectivity in naturally cycling, cigarette-dependent women. *Biology of sex differences, 7*(1), 1-9.

Wilcox, A. J., Dunson, D., & Baird, D. D. (2000). The Timing Of The "Fertile Window" In The Menstrual Cycle: Day Specific Estimates From A Prospective Study. *BMJ: British Medical Journal, 321*(7271), 1259-1262.

Wilding, E. L. (1999). Separating retrieval strategies from retrieval success: an event-related potential study of source memory. *Neuropsychologia, 37*(4), 441-454.

Williams-Gray, C. H., Hampshire, A., Robbins, T. W., Owen, A. M., & Barker, R. A. (2007). Catechol O-methyltransferase Val158Met genotype influences

frontoparietal activity during planning in patients with Parkinson' s disease. *Journal of Neuroscience, 27*(18), 4832-4838.

Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research, 1100*(1), 125-135.

Xu, S. Q., Li, B., Ma, C. Y., & He, L. M. (2014). The Influence of 8-Week Mindfulness Training on Unconscious Emotion Processing. *Chinese Journal of Clinical Psychology, 22*(04), 583-588. [徐少卿, 李波, 马长燕, & 贺兰淼. (2014). 八周正念训练对无意识情绪加工的影响. 中国临床心理学杂志, 22(04), 583-588.]

Yamaguchi, S., & Knight, R. T. (1991). Age effects on the P300 to novel somatosensory stimuli. *Electroencephalography and Clinical Neurophysiology, 78*(4), 297-301.

Yamazaki, M., & Tamura, K. (2017). The menstrual cycle affects recognition of emotional expressions: an event-related potential study. *F1000Research, 6*, 853.

Yang, Z. L., & Zhong, Y. P. (1996). A Review of Three New Methods of Modern Experimental Psychology. *Journal of Psychological Science, 19*(01), 44-48. [杨治良, & 钟毅平. (1996). 现代实验心理学三种新方法评述. 心理科学, (01), 44-48.]

Yuan, K., Yu, D., Cai, C., Feng, D., Li, Y., Bi, Y., . . . Tian, J. (2016). Frontostriatal circuits, resting state functional connectivity and cognitive control in internet gaming disorder. *Addiction biology, 22*(3), 813-822.

Zhuang, J. Y., & Wang, J. X. (2015). The Relationship Between Menstrual Cycles and Women' s Ornamental Behavior. *Advances in Psychological Science, 23*(05), 729-736. [庄锦英, & 王佳玺. (2015). 女性生理周期与修饰行为的关系. 心理科学进展, 23(05), 729-736.]

Zhuang, J. Y., Wang, J. X., Lei, Q., Zhang, W., & Fan, M. (2020). Neural Basis of Increased Cognitive Control of Impulsivity During the Mid-Luteal Phase Relative to the Late Follicular Phase of the Menstrual Cycle. *Frontiers in human neuroscience, 14*, 568399.

Note: Figure translations are in progress. See original paper for figures.