



Phase of the menstrual cycle affects engagement of attention with emotional images

Joanna Pilarczyk*, Emilia Schwertner¹, Kinga Wołoszyn, Michał Kuniecki

Jagiellonian University, Institute of Psychology, Psychophysiology Lab, Poland

ARTICLE INFO

Keywords:

Menstrual cycle
Eye-tracking
Emotion
Attention
Visual perception

ABSTRACT

Changes that occur during the menstrual cycle affect various aspects of behavior, cognition, and emotion. Here, we focused on potential differences between early follicular and midluteal phases in the way women process images of behaviorally relevant content categories: children, threat, disgust, erotic scenes, low- and high-calorie food. Using eye-tracking, we examined women's engagement of attention in the key region of each image in a free-viewing condition. Specifically, we tested how quickly attention was attracted to these regions and for how long it was held there. Participants took part in two experimental sessions, one in the early follicular and one in the midluteal phase. The results showed that in the midluteal phase attention was attracted to the key region earlier than in the early follicular phase: the first fixation more often fell within the key region and there were fewer fixations preceding it. While the effect of the phase in terms of the capture of attention did not depend on the image category, the effect regarding the hold of attention was category-specific, concerning the disgust category only. Specifically, in the midluteal phase the duration of the exploration of the key region between reaching it for the first time and first exiting it was shorter, which might be due to heightened sensitivity to disgusting stimuli in this period. Overall, our results indicate the occurrence of changes in attentional processing of emotional scenes related to the menstrual cycle, which seem to differ depending on the aspect of attention deployment: in the midluteal phase the effect of enhancing orienting was general and concerned any important visual information, whereas the effect of the shortened hold of attention appeared to be limited to specific content.

1. Introduction

Sex hormones, which fluctuate across the menstrual cycle, influence various aspects of emotions, cognition, and behavior (Farage et al., 2008). The most consistent results seem to come from studies on changes linked to emotional processing (Sundström Poromaa and Gingnell, 2014). In the present study, we focused on differences in the engagement of attention with emotional scenes between the early follicular and the midluteal phase of the menstrual cycle.

Emotional stimuli, owing to their significance, are processed in a preferential manner. Emotion-evoking images engage attention more quickly than neutral stimuli (for review see Pourtois et al., 2015), even when located outside of the attentional focus (Calvo and Nummenmaa, 2007; Nummenmaa et al., 2009) or presented for a very short time (Schupp et al., 2004). Emotion-evoking objects within images are found

more quickly and hold attention longer than neutral objects (Humphrey et al., 2012; Pilarczyk and Kuniecki, 2014).

Prioritized processing of visual emotional stimuli might be affected by the phase of the menstrual cycle. There is evidence that sex hormones affect the processing of visual threat cues in a social context (Little, 2013). Some studies on the recognition of facial expressions have demonstrated worse performance in the luteal phase (Derntl et al., 2008a,b; Guapo et al., 2009), for which the major reason was mis-categorization of expressions as anger or disgust, indicating a tendency to interpret social signals as alarming. Other studies, on the other hand, have indicated higher accuracy of emotional face recognition in the luteal phase (Maner and Miller, 2013) as well as higher efficiency of gaze cueing, especially for cues indicating threat (Wolohan et al., 2013). The phase of the menstrual cycle has also been shown to affect the processing of non-social threatening stimuli (Masataka and

* Corresponding author at: Institute of Psychology, ul. Ingardena 6, 30-060, Kraków, Poland.

E-mail addresses: joanna.pilarczyk@uj.edu.pl (J. Pilarczyk), emilia.schwertner@ki.se (E. Schwertner), kinga.b.woloszyn@gmail.com (K. Wołoszyn), michal.kuniecki@uj.edu.pl (M. Kuniecki).

¹ Present affiliation: Center for Alzheimer Research, Division of Clinical Geriatrics, Department of Neurobiology, Care Sciences and Society, Karolinska Institutet, Huddinge, Sweden.

Shibasaki, 2012). Specifically, women reacted more quickly to a threatening stimulus (a snake) located among neutral ones (flowers) in the luteal phase than in the early and late follicular phase. There was no such difference for neutral stimuli, showing that the increase in vigilance in the luteal phase is selective and solely concerns the emotional context. The proposed interpretation of these results refers to higher self-protection motivation in the luteal phase due to the possibility of pregnancy (Derntl et al., 2008a,b; Masataka and Shibasaki, 2012; Maner and Miller, 2013; Wolohan et al., 2013).

This motivation also concerns protecting one's own health. In the luteal phase the immune system is suppressed to prevent the organism from rejecting a developing fetus, which in turn leads to increased susceptibility to infections, analogously to pregnancy (Fessler, 2001; Robinson and Klein, 2012). Thus, the tendency to avoid any possible sources of contagion is intensified, leading to heightened sensitivity to disgusting stimuli (Fessler, 2002; Fleischman and Fessler, 2011; but see also Fessler and Navarrete, 2003). A similar mechanism is considered to be responsible for the prevalence of food aversions during pregnancy (Flaxman and Sherman, 2000). Another line of evidence for the impact of sex hormones on sensitivity to disgust comes from studies which show that when progesterone is high, i.e. during the luteal phase, during pregnancy, and while using some types of oral contraceptives, women exhibit increased preference for facial traits that signal health, such as the lack of pallor (Jones et al., 2005a,b). As this preference does not depend on the gender of the depicted person, the effect probably is not related to mating preferences, but is instead a protective mechanism to reduce the risk of infection (Jones et al., 2005b).

Heightened nausea sensitivity is also linked to changes in eating habits and food preferences. During the luteal phase women are more likely to exhibit food aversions, especially if a given food may be the source of pathogens (e.g., meat; reviewed in Fessler, 2001). On the other hand, during this phase the intake of calories increases (Barr et al., 1995), as does the subjective rating of the appeal of food, compared to the second week of the menstrual cycle (Frank et al., 2010). Moreover, Frank and collaborators have demonstrated that brain response to food images differs between the phases, with high-calorie food producing greater orbitofrontal cortex and mid cingulum activations than low-calorie food in the luteal phase as compared to the follicular phase.

Reactions to other categories of positive stimuli also seem to be affected by sex hormones. For example, in the study by Dreher et al. (2007), during the midfollicular phase anticipated and actual monetary rewards evoked higher activation of the reward system, a reaction which was related to the estrogen level. Nevertheless, it is not clear whether the effect of hormone levels and menstrual phase can be generalized to all classes of positive stimuli.

A distinctive, but rarely studied, class of biologically-relevant positive stimuli is children. Baby schema (Lorenz, 1943), a set of facial features typical of newborns, elicits positive emotions in observers and automatically captures their attention in early stages of visual processing (Brosch et al., 2008). Interestingly, the effect of spatial orienting towards baby faces is as strong as it is for fear-inducing stimuli, suggesting a robust biological underpinning of this effect. Hahn et al. (2015) showed that hormonal level, namely of testosterone, is positively correlated with the perception of children's cuteness. The contribution of the phase of the menstrual cycle in perception of children is, however, unknown.

Erotic images are another category which appears worth exploring for its relationship with the menstrual cycle. Although various studies have shown that perception of erotic stimuli depends in general on the gender of the viewer (e.g., Sabatinelli et al., 2006; Bradley et al., 2015) and sex hormones (Rupp and Wallen, 2007a), the possible modulatory effect of menstrual phase on the interest in sexually explicit images has not been clearly established. An eye-tracking study by Rupp and Wallen (2007b) provided no evidence for the influence of the menstrual phase on fixation ratios to specific regions of erotic scenes. The authors,

however, argue that since normally cycling women attended more to genitals and less to the background of a scene than women using hormonal contraception, sex hormones do affect engagement of attention with erotic stimuli. Although the follow-up study (Wallen and Rupp, 2010) again showed no main effect of menstrual phase on the interest in sexual scenes, menstrual phase was not irrelevant as viewing erotic stimuli for the first time in the luteal phase, compared to the periovulatory phase, predicted lower interest in these stimuli in subsequent viewing sessions, regardless of the current menstrual phase.

In summary, there is growing evidence that physiological changes which in the luteal phase prepare the woman's body for possible pregnancy are accompanied by psychological changes induced by the same hormonal fluctuations. The observed psychological changes include enhanced social monitoring (Maner and Miller, 2013) and preference for high-calorie food (Frank et al., 2010), increased vigilance to physical threat (Masataka and Shibasaki, 2012), sensitivity to sources of contagion (Fessler, 2002; Jones et al., 2005a,b; Fleischman and Fessler, 2011), as well as reduced activity of the reward system (Dreher et al., 2007). In this study we aimed to examine whether the above changes are manifested in the form of differences in deployment of visual attention to various types of emotional stimuli previously shown to be related to sex hormones, such as threat, disgust, children, erotic scenes, and high- and low-calorie food. To this end two aspects of the deployment of attention were analyzed, specifically how fast and effectively emotional stimuli attract attention (capture of attention) and for how long the focus of attention lingers over the stimuli (hold of attention). We expected that in the midluteal phase, compared to the early follicular one, attention to threat stimuli would be enhanced, while disgust stimuli would be avoided. We also hypothesized that attending to high-calorie food would be facilitated, but no difference in the low-calorie food would be observed. As for children and erotic scenes, the impact of menstrual phase is unresolved, however reduced activity of the reward system in the luteal phase might suggest lower interest in these positive categories, and thus we expected reduced attention towards them in the midluteal phase.

2. Materials and methods

2.1. Participants

The recruitment consisted of several stages. In the initial step, female volunteers were asked to complete an online application form. Women who regularly menstruated, were heterosexual, were not pregnant at that time, did not have children, did not use hormonal contraception, and had no diagnosis of any endocrine disease were invited to participate in the study. In the follicular phase, participants were provided with a set of ovulation (LH) tests to be used in the middle of their cycle to determine the occurrence of ovulation. Participants who did not report positive result on any of the ovulation (LH) tests were excluded from the study. In total, twenty participants aged between 19 and 34 ($M = 24$, $SD = 3.3$) with regular menstrual cycles ($M = 29.5$ days, $SD = 2.2$) completed both experimental sessions. Before each session, all participants signed an informed consent. The experimental procedures were approved by the local ethics committee.

2.2. Stimuli

A set of 120 colored images were selected from databases of emotional images, such as the International Affective Picture System (IAPS; Lang et al., 2005), the Nencki Affective Picture System (NAPS; Marchewka et al., 2014), the Geneva Affective Picture Database (GAPED; Dan-Glauser and Scherer, 2011), and from the internet. All belonged to one of six categories: threat, disgust, children, erotic scenes, low-calorie food, and high-calorie food, with 20 images representing each of them (Fig. 1). Analogously to the study by van Hoof et al. (2013), images from the threat category depicted aggressive

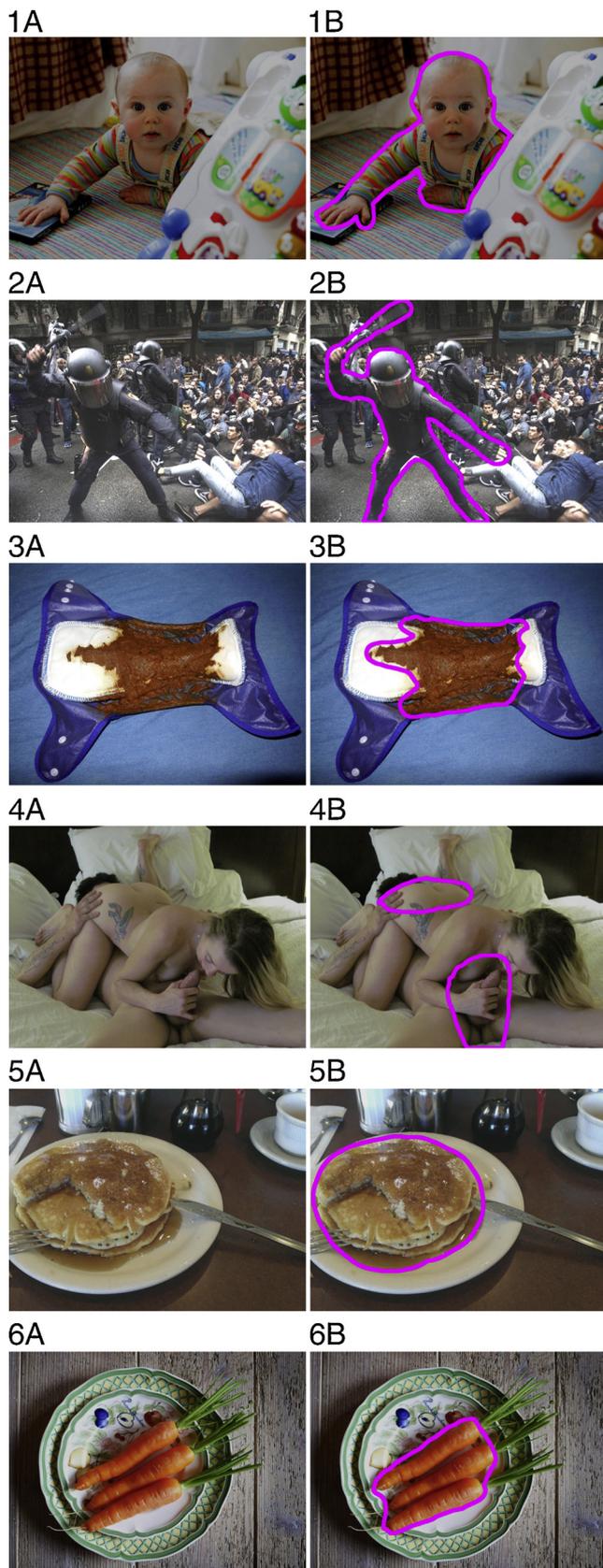


Fig. 1. Image categories. Examples of images (left) with corresponding regions of interest (ROIs) circled in pink (right) belonging to categories (1A - 1B) Children, (2A - 2B) Threat, (3A - 3B) Disgust, (4A - 4B) Erotic scenes, (5A - 5B) High-calorie food, and (6A - 6B) Low-calorie food. Presented images are similar to the ones used in the study in terms of their content, contrast and luminance, and ROIs size. Images were downloaded from the Internet on the Creative Commons License (see Acknowledgements for full information regarding images' authors and sources).

sexual intercourse. Low-calorie food was represented by raw fruits and vegetables, and high-calorie food by high-fat fried dishes and desserts (see Frank et al., 2010). Images of children depicted a baby or a toddler whose face was visible. Prior to the study, the experimenter determined the key object (region of interest, ROI) for each image. On average, ROI covered 13.5 percent (SD = 6.7) of the total image area. Importantly, images were deliberately selected to contain, along with the key object, objects that did not belong to the given category (e.g., a vase with flowers in a high-calorie food image), thus allowing attention to be focused on a rival object. Finally, all images were equalized (using Adobe Photoshop) in terms of luminance and contrast, respectively measured as mean and standard deviation of the $L^*a^*b^*$ color space.

2.3. Procedure

All participants attended two experimental sessions: during the early follicular and during the midluteal phase of their menstrual cycle. The order of the experimental sessions was counterbalanced: 11 and 9 women underwent the first experimental session in their midluteal phase and early follicular phase, respectively. The interval between the two sessions was approximately two weeks (similarly to Goldstein, 2005). The early follicular phase was defined as days 4 to 6 of the menstrual cycle, and the midluteal phase was defined as 6 to 8 days following ovulation, similarly to Amin et al. (2006) and Dreher et al. (2007), the occurrence of which was determined using ovulation (LH) tests given to the participants beforehand. Prior to each session, saliva samples (approx. 1.5 ml) were collected to confirm the menstrual phases in the progesterone level assays. To avoid saliva contamination, subjects were asked to refrain from eating for 2 h and not to drink coffee for 30 min before each the sessions. As progesterone fluctuates diurnally (Syrop and Hammond, 1987; Kottler et al., 1989), experimental sessions were held at about the same time of the day, that is, between 4 and 8 pm. Saliva samples were collected and stored using Salitubes (DRG Diagnostic GmbH, Marburg, Germany). The Salitubes were frozen at $-20\text{ }^{\circ}\text{C}$ immediately after collection and stored until the assay. The assays were conducted by the Department of General Biochemistry, Jagiellonian University, Kraków, Poland. Enzyme-linked immunosorbent assays were used for the saliva analyses (DRG Diagnostics GmbH, Marburg, Germany). The analytical sensitivity for progesterone was 3.8 pg/ml.

The eye-tracking study was divided into 4 blocks with self-paced breaks between each of them, during which participants could rest their eyes, change the position, etc. Each block consisted of 30 images and each image was presented for 5 s, preceded by a central fixation cross displayed for a random interval of 300–800 ms and calibration and validation procedures. Stimuli presentation was fully randomized across subjects and experimental sessions, to avoid order repetition effects. The entire experimental procedure took up to 25 min. The experimental procedure was programmed using Eyelink Experiment Builder (SR Research, Ontario, Canada). Stimuli were presented on a 21-inch TFT monitor. Each picture covered 23 deg. of the visual field in width and 17.5 deg. in height. The monitor was calibrated using ColorMunki (X-Rite, 131 Michigan, USA) to the white point CIE Illuminant D65 and luminance of 120 cd/m². Participants were seated 73 cm from the computer screen with their head position stabilized

people or animals, while disgust images depicted contamination (e.g., dirty toilets, maggots, decay), bodily fluids (e.g., vomiting), and skin conditions. Erotic scenes depicted heterosexual couples engaging in

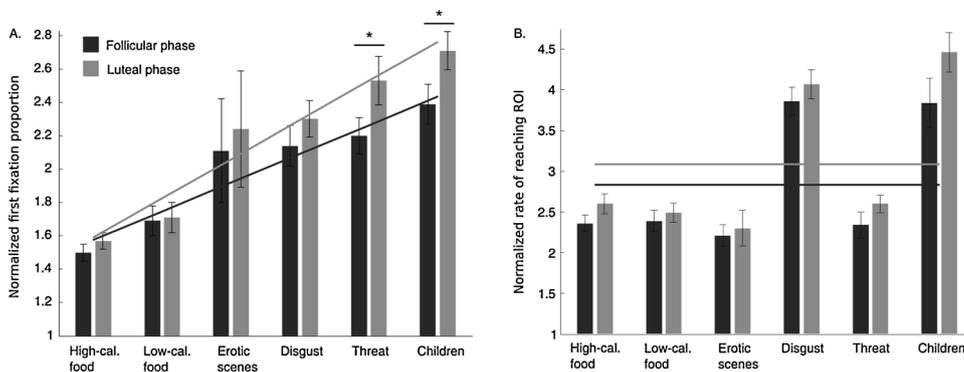


Fig. 2. Capture of attention. (A) Normalized first fixation proportion that fell within the region of interest (ROI) of each image category in the early follicular and midluteal phase. Lines represent linear interaction between menstrual phase and image category. Arbitrary units represent how many times more fixations fell within an ROI than can be attributed to chance. (B) Normalized rate of reaching ROI of each image category in the early follicular and midluteal phase. Lines represent means for menstrual phases averaged across image categories. Arbitrary units represent how many times fewer fixations were made before entering the ROI than can be attributed to chance. Asterisks denote significant differences in pairwise comparisons; * $p < .05$, ** $p < .01$. Error bars in both graphs represent standard error.

with a chinrest. The information given to the participants instructed them to freely explore the presented scenes with no task specified.

After the second experimental session, participants were asked to rate the valence and arousal of each image presented in the study on the 9-point Self-Assessment Manikin (SAM) scale (Bradley and Lang, 1994). For the rating procedure, images were displayed on a 14-inch flat panel computer screen in random order without any temporal limit. Presentation of each image was terminated by a button press and was followed by the SAM scales for rating.

2.4. Eye movement recording and analysis

Eye position was recorded with an infrared remote Eyelink 1000 (SR Research) eye tracker that sampled pupil position at 500 Hz. The position of both eyes was recorded, but only the data from the better-calibrated eye was analyzed. A 9-point calibration and validation procedure was repeated at the beginning of each experimental block and whenever drift check showed calibration inaccuracy. Average calibration error of the analyzed eye was 0.36 deg. (SD = 0.11). Fixations and saccades were detected using the default Eyelink 1000 algorithm. Saccades were defined as deflections greater than 0.15 deg., velocity exceeding 30 deg./s, and acceleration over 8000 deg./s². Fixations were defined as periods between saccadic eye movements. Although we did not set a duration threshold to eliminate microfixations, fixations lasting over 100 ms comprised more than 95% of the analyzed data. Eye-tracking data preprocessing was conducted using MATLAB (The MathWorks, Natick, MA, USA).

We calculated two parameters of attention capture, namely the location of the first fixation in each image according to whether it fell in an ROI (normalized first fixation proportion, nFFP) and the number of fixations made before entering an ROI (normalized rate of reaching ROI; nRRR). Hold of attention was measured as the sum of durations of consecutive fixations within an ROI executed in the period between entering and exiting it for the first time (normalized first-pass duration; nFPD). Since the chance of fixating on a particular region of an image does not depend solely on the content of the picture but also on the size of the region and its distance from the center of an image (Tatler, 2007), it is essential to account for these factors. Therefore, each raw measure was transformed to its normalized form (Pilarczyk and Kuniecki, 2014), which compensated for both the size of the ROI and participants' tendency to scan central areas of an image more often than its peripheries. In brief, the normalized first fixation proportion (nFFP) is calculated by dividing (separately for each participant, image category, and menstrual cycle phase) the fraction of fixations which fell within ROIs (positive sample) by the fraction of fixations executed within the same location by the same person during the same session in response to other images from the given category (negative sample).

The same logic was applied to the first-pass duration and the rate of reaching an ROI. In effect, if the normalized index equals one, the location of the first fixation, the number of fixations until reaching an ROI, or the durations of fixations in a given ROI can be explained solely by the ROI's size and location. If it is larger than one, more fixations fell in an ROI, their durations in the ROI are longer, or fewer fixations are made before entering a given ROI than predicted by those factors. Importantly, such normalization enables direct comparisons between image categories, disregarding any differences in an ROI's size or location.

Statistical analyses were conducted using SPSS (SPSS, Inc., Chicago, Illinois, USA). Data were analyzed using a repeated measures ANOVA design with factors of image category (high-calorie food, low-calorie food, erotic scenes, disgust, threat, children) and menstrual phase (early follicular, midluteal). Additionally, to check for effect of session order, we conducted repeated measures ANOVA with factors of session order (first and second session) and image category (six categories). The level of progesterone in the early follicular and midluteal phases was compared using a paired samples t-test. For all statistical tests, when the assumption of sphericity was violated, Huynh-Feldt correction was used, whereas Bonferroni correction was used for simple effects tests and post-hoc tests.

3. Results

The progesterone level measured during the experimental sessions was significantly higher in the midluteal phase ($M = 260$ pg/ml, $SD = 144$) than in the early follicular phase ($M = 95$ pg/ml, $SD = 66$), $t(19) = 5.78$, $p < .001$. The intra-assay coefficient of variation was 9%. The levels of progesterone did not correlate significantly with any measure of visual attention used in this study (see Supplementary materials, Table S1).

Capture of attention was assessed using two measures: proportion of first fixations falling in the ROI (nFFP, Fig. 2A; for descriptive statistics see Supplementary materials, Table S2) and the number of fixations made before entering an ROI (nRRR, Fig. 2B; for descriptive statistics see Supplementary materials, Table S3). Both measures were affected by image category ($F(5,95) = 10.08$, $p = .001$, $\eta^2 = 0.347$; $F(5,95) = 48.78$, $p < .001$, $\eta^2 = 0.72$ respectively; see Supplementary materials, Tables S5 and S6) and menstrual cycle phase ($F(1,19) = 5.03$, $p = .037$, $\eta^2 = 0.209$; $F(1,19) = 5.58$, $p = .029$, $\eta^2 = 0.227$ respectively), with increased general capture of attention in the midluteal phase. Moreover, in the case of nFFP, if the categories were aligned according to increasing nFFP score, the interaction between image category and menstrual phase emerged, as validated by the significant ANOVA linear trend ($F(1,19) = 5.96$, $p = .025$, $\eta^2 = 0.239$): the more attention was attracted by a given category on

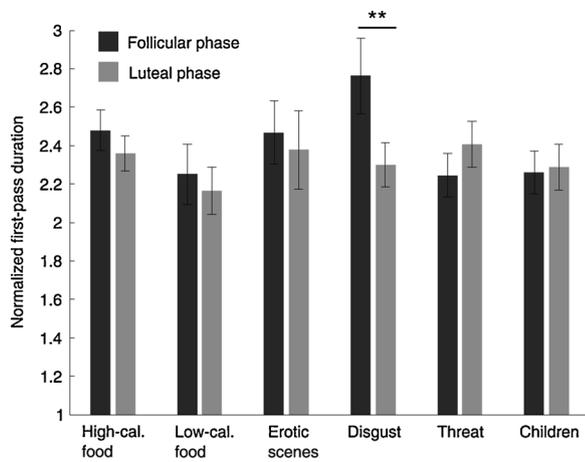


Fig. 3. Hold of attention. Normalized first-pass duration within the region of interest (ROI) of each image category in the early follicular and midluteal phase. Arbitrary units represent how many times longer were first-pass durations than can be attributed to chance. Asterisks denote significant differences in pairwise comparisons; * $p < .05$, ** $p < .01$. Error bars represent standard error.

average, the greater was the difference in nFFP between the phases (Fig. 2A). Simple effects comparison showed significant differences between menstrual phases in the threat ($p = .025$) and children ($p = .011$) categories. For the nRRR this interaction was not significant ($F(5,95) = 1.16, p = .34, \eta^2 = 0.057$).

Hold of attention (Fig. 3) was examined by calculating normalized first-pass duration in ROI (nFPD; for descriptive statistics see Supplementary materials, Table S4). The nFPD (Fig. 3) did not differ between the phases ($F(1,19) = 2.04, p = .17, \eta^2 = 0.097$) or image categories ($F(5,95) = 1.15, p = .34, \eta^2 = 0.057$). The interaction of these factors, however, was significant ($F(5,95) = 2.68, p = .041, \eta^2 = 0.12$). Follow-up simple effects analysis revealed a significant difference between menstrual phases in the disgust category only ($p = .003$), with smaller nFPD in the midluteal phase (for an example of fixation distribution on an image see Supplementary materials, Figure S1). In other image categories the effect of menstrual phase was non-significant ($p > .13$).

In the analyses regarding effects of session order no main effects of session, nor any significant interactions between factor of image category and session order were found. Normalized first fixation proportion (nFFP) did not differ between sessions ($F(1,19) = 1.67, p = .21, \eta^2 = .08$) and there was no interaction between image category and session order ($F(5,95) = 0.44, p = .69, \eta^2 = .02$). Also in case of normalized rate of reaching ROI (nRRR) the effect of session order ($F(1,19) = 1.09, p = .31, \eta^2 = 0.05$) and the interaction between session order and image category ($F(5,95) = 0.26, p = .94, \eta^2 = .01$) were non-significant. The normalized first-pass duration (nFPD) did not differ between sessions ($F(1,19) = 0.02, p = .90, \eta^2 < 0.01$) and we found no interaction between session order and image category ($F(5,95) = 1.15, p = .34, \eta^2 = 0.06$).

Participants' evaluation of presented images yielded ratings of valence and arousal for each image category presented in Table 1.

4. Discussion

The results of our study add to the evidence for the influence of the menstrual cycle on the processing of emotional material. Our findings indicate that the phase of the menstrual cycle affects gaze location and duration on the key object in a scene.

Specifically, the study showed that in the midluteal phase the first fixation on a scene, independently of the scene category, is more likely to fall on a key object than in the early follicular phase. Since fixations

Table 1

Valence and arousal ratings of the images presented in the study.

| Image category | Mean valence (SD) | Mean arousal (SD) |
|-------------------|-------------------|-------------------|
| High-calorie food | 6.51 (.55) | 3.26 (.31) |
| Low-calorie food | 6.51 (1.07) | 4.11 (.45) |
| Erotic scenes | 5.15 (.56) | 5.68 (.27) |
| Disgust | 3.18 (.50) | 5.31 (.62) |
| Threat | 3.34 (.53) | 5.52 (.45) |
| Children | 6.22 (.63) | 3.54 (.42) |

Valence ranges between 1 (unpleasant) and 9 (pleasant). Arousal ranges between 1 (calm) and 9 (excited).

up to 500 ms after image onset are generally not under voluntary control (Calvo et al., 2008), the observed effect can be attributed to automatic capture of attention. Furthermore, this effect depended on the category of visual stimuli, which indicates the modulatory role of the scene's meaning. The factor that accounts for the observed differences across categories seems to be the strength with which the given category of an image captures attention on average. Our results showed that the more attention-capturing was a particular category, the larger was the difference between the menstrual phases, with a higher ratio of first fixations in ROIs in the midluteal phase. This pattern of results might be interpreted as the effect of the general enhancement of attention deployment to important stimuli in the midluteal phase. The most pronounced difference between the phases was observed for images depicting children and threat, which were the categories with the highest index of first fixations that fell in an ROI on average.

This pattern of results corresponds to the effect observed in the EEG study by Brosch et al. (2008) in which they presented participants with basic negative and positive stimuli depicting, respectively, angry faces and baby faces. Focusing on P1, an early event-related potential that has previously been shown to be related to the strength of attention deployment (e.g., Luck et al., 2000), Brosch and collaborators observed that attentional engagement is equally strong for both categories. These results indicate that threatening stimuli and children's faces are equally capable of rapidly attracting attention, presumably owing to their high biological relevance (Brosch et al., 2008). The increase in deployment of attention to children in the midluteal phase observed in our study might be related to the increased activity of the highly conserved biological nursing mechanism during the period when conception is possible. It is, however, unclear which particular hormones that fluctuate across the menstrual cycle may cause such an effect. The hormonal underpinning of parental care in humans is not fully understood, but most likely it involves heightened levels of oxytocin and prolactin (Rilling, 2013). Nevertheless, although concentration of prolactin in the luteal phase is indeed higher than it is in the follicular phase (Franchimont et al., 1976), the concentration of oxytocin is lower (Salonia et al., 2005).

Another manifestation of the enhancement of attention to emotional objects in the midluteal phase observed in our study is the lower number of fixations made before entering the region of interest, compared to the early follicular phase; in other words, in the midluteal phase participants directed their eyes to the most crucial information within a scene more quickly than in the early follicular phase. Since this effect was category nonspecific, it supports the hypothesis that proposes elevated vigilance towards any emotional information during the midluteal phase. This seems to correspond to the findings that women in the luteal phase are more sensitive to target stimuli linked to emotional cues, that is, facial expressions with averted gaze, than are women in the follicular phase (Wolohan et al., 2013). The authors suggested that this hypersensitivity is related to the adaptive mechanism of fetal development protection. Here, we extend these findings by showing for the first time that the capture of attention by emotional cues in the midluteal phase is a more general tendency, also present in the case of complex visual scenes, including non-social ones.

However, due to lack of neutral category of images in our experimental design, such as man-made everyday objects, it is not clear whether this enhancement of attention extends to all objects or only emotionally relevant ones.

The hypothesis that hormonal changes related to the menstrual cycle would affect the distribution of fixations also in the case neutral images is plausible in the light of previous studies on the influence of the menstrual cycle on attention and memory. Particularly, research shows that women in the luteal phase exhibit lower tendency to process the gist and higher tendency to process details of material, in the case of both affective information, such as emotional stories (Nielsen et al., 2013), and neutral information, such as Navon figures (Pletzer et al., 2014). This shift in attention, from global to local features, which has been observed in the luteal phase seems related to progesterone (Pletzer et al., 2014) and testosterone (Nielsen et al., 2013; Pletzer et al., 2014). The results of our study seem to suggest reverse trend, that is women in the luteal phase were faster and more efficient at directing their attention to the central, gist-related features, i.e., the key objects, rather than to the peripheral details, i.e., the background of an image. These effects were not correlated to progesterone (Table S1). Since in the present study no other hormones were measured, it is not possible to determine whether the observed tendencies can be ascribed to fluctuations in any particular hormone or an interaction of several hormones, which can be considered a limitation of our study.

Possible brain underpinnings of the increased efficiency of attention deployment to emotional objects in the midluteal phase might involve the influence of sex hormones, including estrogen, progesterone and its metabolites, on the activity of several brain structures linked to emotional response, such as the amygdala, inferior frontal gyrus, dorsolateral prefrontal cortex, ventromedial prefrontal cortex, and orbitofrontal cortex (Protopopescu et al., 2005; Dreher et al., 2007; Ossewaarde et al., 2010; Zeidan et al., 2011; for reviews see Toffoletto et al., 2014 and Lisofsky et al., 2015). Of particular importance might be changes in the amygdala's responsiveness, which is known to fluctuate across the menstrual cycle (Goldstein, 2005; Derntl et al., 2008b; Andreano and Cahill, 2010). The amygdala is not only the fear center (Phelps et al., 2005), but it is also linked to the selection of important information (Pessoa and Adolphs, 2010). Importantly, numerous studies have demonstrated that the amygdala modulates perception and attention to emotional stimuli and it is speculated that this might happen through the re-entrant connections from the amygdala to the visual cortex (Bradley et al., 2003; Kuniecki et al., 2018; Lang et al., 1998; Pourtois et al., 2013; Todd, Cunningham et al., 2012; Todd and Anderson, 2009), whose existence was documented in both humans (Catani et al., 2003; Gschwind et al., 2012) and macaques (Amaral et al., 2003). Direct influence of sex hormones on the amygdala plausible since this structure features the receptors of ovarian hormones (Osterlund and Hurd, 2001). In a meta-analytic study, Lisofsky et al. (2015) showed that in the luteal phase the left amygdala and the left hippocampus are more strongly activated, whereas in the follicular phase higher activity is observed in the right amygdala and the right hippocampus. The meta-analysis by Toffoletto et al. (2014) also provided some evidence for higher reactivity of the left amygdala during encoding and retrieval of negatively valenced stimuli in the midluteal phase. The left hemisphere amygdala is more strongly linked to encoding and long-term memory for arousing pictures in women relative to men (Cahill et al., 2004). In combination, the evidence for the higher reactivity of the left amygdala in the luteal phase and its link to the processing of emotional content by women suggests that the amygdala is the hypothetical neural base of the observed effect of enhanced attention capture by emotional objects in the luteal phase. Consistent results come from the fMRI study by Protopopescu et al. (2005) which demonstrated that in the late luteal phase, compared to the late follicular phase, the activity of the medial orbitofrontal cortex (OFC) is enhanced. Since it is an area which has strong connections with subcortical regions of the limbic system, the greater activity within this

region might suggest stronger engagement of the limbic system in reaction to negative stimuli in the premenstrual period (Protopopescu et al., 2005). Another brain structure whose activity is modulated by ovarian hormones fluctuating across the menstrual cycle is the inferior frontal gyrus, involved in attending to negative stimuli (for review see Toffoletto et al., 2014). Furthermore, the increased vigilance observed in our study could be related to premenstrual symptoms such as tension, irritability, or anxiety, which are experienced at different intensities by a lot of healthy women in the luteal phase (for a review see Farage et al., 2008). In particular, during the luteal phase a non-specific increase of arousal is observed (Becker et al., 1982), along with heightened stress response in the late luteal phase to factors like negative visual stimuli (Ossewaarde et al., 2010), physical stressors (Tersman et al., 1991), and mental effort (Tersman et al., 1991; Kumari and Corr, 1998). However, we did not employ any measure of premenstrual symptoms, and therefore we cannot determine the impact of elevated arousal and stress response on the increased attention to emotional stimuli.

The results described above indicate the occurrence of changes in attentional engagement across the menstrual cycle. Nevertheless, these alterations appear to be limited to attention capture. Our results do not show any category non-specific effect regarding the duration of the hold of attention. In the case of attentional hold, the only significant difference was observed in the disgust category, with smaller normalized first-pass duration index in the midluteal phase, indicating shorter hold of attention than can be expected by chance. Shorter first-pass duration signifying faster disengagement of attention can be attributed to heightened reactivity to disgusting stimuli and stronger avoidance of disgusting objects in the luteal phase. This finding is in line with previous research that has demonstrated increased sensitivity to disgusting stimuli when progesterone is high (Fessler, 2002; Fleischman and Fessler, 2011). Nevertheless, on the basis of our results, we are not able to refute the possibility, however unlikely, that this effect is in fact due to heightened interest in disgusting stimuli in the early follicular phase. Another explanation of this effect could be related to possible enhanced motivation to seek new information in the luteal phase, leading to shorter focus of gaze on the disgusting object in order to explore the rest of the image. However, in such case shorter first-pass durations should have been observed in more than one category of images. This explanation would be also contradictory to results obtained by Colzato et al. (2012) who show that elevated tendency to attend to new information, manifested by stronger inhibition of return to previously attended location, can be observed in the late follicular phase, when estrogen is high, but not in the luteal phase.

The measure of hold of attention seems to be particularly relevant to disgust-evoking images, which in the general population hold the focus of attention for longer than fear-evoking images (van Hoof et al., 2013). Interestingly, attention bias to disgust-evoking images is not dependent on the individual characteristics of female participants, such as disgust sensitivity or anxiety (van Hoof et al., 2014). However, those authors did not take into consideration the menstrual phase of the participants. Our study suggests that this factor is significant, and that disengagement of attention from disgusting objects seems to be facilitated in the midluteal phase.

It is worth to mention also some limitations of our study. One of them is our choice to include only two phases of the menstrual cycle. Comparison between early follicular and midluteal phases, due to large differences in hormonal levels between these phases, is quite common in the research on the effects of menstrual cycle on emotion and cognition, which makes it easy to link the obtained results to the existing literature. However, such choice might cause some specific effects to remain undetected. For example, directing attention towards the erotic images might be particularly enhanced during peri-ovulatory phase, while not differing between the early follicular and midluteal phases. Another example are images depicting food, for which we did not observe any category-specific effects. The effect of menstrual phase in the

case of those images, particularly the ones belonging to the high-calorie food category, might be highly specific and limited to the late follicular phase as compared to all other time points during the cycle, which would be in line with the results of the study by Frank et al. (2010). Therefore, including peri-ovulatory or late follicular phases to the experimental design could be beneficial in further studies, especially in those focusing on the above-mentioned categories of stimuli. However, including too many experimental sessions, and therefore exposing participants to the same stimuli numerous times, especially if done over short period of time, might cause significant session-order effects. Such effects might be of interest in some experiments, for example those specifically designed to assess interest in erotic stimuli in consecutive sessions or the significance of the menstrual phase during the first exposure to the set of erotic images. The studies on the repeated presentation of erotic images produced mixed results, showing either lack of session order effect (Rupp and Wallen, 2007b; Wallen and Rupp, 2010) or a main effect of session order, averaged across all experimental groups (males, females using oral contraception and normally cycling females; Rupp and Wallen, 2007a). In our study the session order effects were not present in any category, including erotic images.

Finally, it is worth stressing that all presented stimuli were complex real-life scenes, rather than schematic objects such as snakes and flowers. In each image, apart from the key object belonging to the studied category, other objects were also present. Such images are well suited to studying the capturing and holding of attention because they depict competing objects that may also draw attention. Moreover, presenting real-life images creates more ecologically valid conditions in which the mechanisms of visual attention usually operate, thus facilitating their expression. In many studies (e.g., Conway et al., 2007; Derntl et al., 2008a,b; Wolohan et al., 2013) the effects of the menstrual cycle on the processing of threat and other evolutionary-relevant stimuli were examined using emotional faces. Since face processing is a unique mechanism that involves specialized brain structures (for a review see Dekowska et al., 2008), it is difficult to draw general inferences from studies using only facial stimuli. Studies using non-facial stimuli are rare and usually involve presenting simplified isolated stimuli (e.g., Matasaka and Shibasaki, 2012). In addition, including several emotional categories of real-life images allowed us to pinpoint both general and category-specific mechanisms of attentional differences related to menstrual cycle, broadening our conclusions.

The other aspect that seems important to note here regards the measurement of the hormones. Firstly, since we did not test the estradiol level, we cannot fully attribute the effects concerning the processing of emotional material to the level of the ovarian hormones. Although based on previously reported results (for reviews see Farage et al., 2008; Little, 2013; Sundström Poromaa and Gingnell, 2014) the link between attentional processing of emotional stimuli and ovarian hormones seems valid, we cannot exclude the eventuality that such influence is indirect. The effects regarding attention might be secondary to the hormonally mediated changes in other psychological factors, like emotional state, more general changes in affective processing, or they might be caused by other aspects of hormonal milieu specific for each phase. For example, it would be worth to assess the testosterone to explore the connection shown by Pletzer et al. (2014) between testosterone and progesterone level with attention, described earlier in the discussion. The fact that our study does not allow to directly link the differences in the processing of emotional scenes to the level of particular hormones, makes it also necessary to be cautious in making predictions regarding other states associated with particular level of estrogen and progesterone, such as pregnancy, menopause or use of hormonal contraception. Additionally, similarly to numerous other studies, ours involved only young, healthy women. It would be vital to extend future research to women suffering from clinical conditions, with severe premenstrual syndrome (PMS) and premenstrual dysphoric disorder (PMDD) being of particular interest (see Halbreich et al., 2003), and to take into account age-related changes.

The results of our study substantiate the idea of the modulatory role of the menstrual cycle on visual attention. In particular, we have demonstrated that the key objects of complex images attract attention more efficiently during the midluteal phase. The effect of the menstrual cycle was observed as early as at the very first fixation on a scene, suggesting low-level automatic attentional bias. Moreover, the enhancement of attention capture by key visual information in the midluteal phase seems to be unspecific as it transpired in images belonging to various semantic categories. The attentional bias in the midluteal phase was particularly pronounced in categories that, in general, strongly attracted attention. Thus, the potential function of this bias involves directing attention to particularly important objects in the visual environment. In contrast, hold of attention was affected by menstrual phase in a category-specific manner as it differed only in the case of disgust-evoking images. Faster disengagement of attention from disgusting objects can be interpreted as an evidence for the enhanced avoidance of possible sources of contagion in the midluteal phase. In combination, our results indicate that visual attention can be modulated in both a generalized and specialized manner by the phase of the menstrual cycle.

Declarations of interest

None.

Acknowledgements

This work was supported by the National Science Center in Poland [grant number 2014/15/N/HS6/04179] and Bratniak Student and Alumni Foundation of Jagiellonian University.

In Fig. 1 we present images retrieved September 19, 2018 from the Internet on the Creative Commons License: image1 - CC0 license, source <https://www.publicdomainpictures.net/en/view-image.php?image=21689&picture=toddler-playing> (cropped); image 2 - CC BY-SA 3.0 license, author Robert Bonet, source https://en.wikipedia.org/wiki/Police_brutality#/media/File:Cargas-Sardenya-Diputacio-Ramon-Llull_EDIIMA20171001_0193_19.jpg (cropped); image 3 - CC BY-SA 3.0 license, author ParentingPatch, source https://commons.wikimedia.org/wiki/File:Prune_Toddler_Baby_Poop_in_Best_Bottom_Diaper.JPG; image 4 - CC BY 2.0 license, author Jon Photographer, source https://en.wikipedia.org/wiki/File:Couple_69_sex_position_on_bed.jpg; image 5 - CC0 license, source <https://pixabay.com/pl/nale%C5%9Bniki-%C5%9Bniadanie-syrop-posi%C5%82ek-951029/> (cropped); image 6 - CC0 license, source <https://www.maxpixel.net/Woods-Food-Gourmet-Vegetables-Healthy-Table-Wood-3095066> (cropped).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.psyneuen.2019.02.009>.

References

- Amin, Z., Epperson, C.N., Constable, R.T., Canli, T., 2006. Effects of estrogen variation on neural correlates of emotional response inhibition. *NeuroImage* 32 (1), 457–464.
- Andreano, J.M., Cahill, L., 2010. Menstrual cycle modulation of medial temporal activity evoked by negative emotion. *NeuroImage* 53 (4), 1286–1293.
- Barr, S.I., Janelle, K.C., Prior, J.C., 1995. Energy intakes are higher during the luteal phase of ovulatory menstrual cycles. *Am. J. Clin. Nutr.* 61 (1), 39–43.
- Becker, D., Creutzfeldt, O.D., Schwibbe, M., Wuttke, W., 1982. Changes in physiological, EEG and psychological parameters in women during the spontaneous menstrual cycle and following oral contraceptives. *Psychoneuroendocrinology* 7 (1), 75–90.
- Bradley, M.M., Lang, P.J., 1994. Measuring emotion: the self-assessment Manikin and the semantic differential. *J. Behav. Therapy Exp. Psychiatry* 25, 49–59.
- Bradley, M.M., Costa, V.D., Lang, P.J., 2015. Selective looking at natural scenes: hedonic content and gender. *Int. J. Psychophysiol.* 98 (1), 54–58.
- Brosch, T., Sander, D., Pourtois, G., Scherer, K.R., 2008. Beyond fear: rapid spatial orienting toward positive emotional stimuli. *Psychol. Sci.* 19 (4), 362–370.

- Cahill, L., Uncapher, M., Kilpatrick, L., Alkire, M.T., Turner, J., 2004. Sex-related hemispheric lateralization of amygdala function in emotionally influenced memory: an fMRI investigation. *Learn. Mem.* 11, 261–266.
- Calvo, M.G., Nummenmaa, L., 2007. Processing of unattended emotional visual scenes. *J. Exp. Psychol. Gen.* 136 (3), 347–369.
- Calvo, M.G., Nummenmaa, L., Hyönä, J., 2008. Emotional scenes in peripheral vision: selective orienting and gist processing, but not content identification. *Emotion* 8 (1), 68–80.
- Colzato, L.S., Pratt, J., Hommel, B., 2012. Estrogen modulates inhibition of return in healthy human females. *Neuropsychologia* 50 (1), 98–103.
- Conway, C.A., Jones, B.C., DeBruine, L.M., Welling, L.L.M., Law Smith, M.J., Perrett, D.I., Sharp, M.A., Al-Dujaili, E.A.S., 2007. Salience of emotional displays of danger and contagion in faces is enhanced when progesterone levels are raised. *Horm. Behav.* 51 (2), 202–206.
- Dan-Glauser, E.S., Scherer, K.R., 2011. The Geneva affective picture database (GAPED): a new 730-picture database focusing on valence and normative significance. *Behav. Res. Methods* 43, 468–477.
- Dekowska, M., Kuniecki, M., Jaśkowski, P., 2008. Facing facts: neuronal mechanisms of face perception. *Acta Neurobiol. Exp.* 68, 229–252.
- Derntl, B., Kryspin-Exner, I., Fernbach, E., Moser, E., Habel, U., 2008a. Emotion recognition accuracy in healthy young females is associated with cycle phase. *Horm. Behav.* 53, 90–95.
- Derntl, B., Windischberger, C., Robinson, S., Lamplmayr, E., Kryspin-Exner, I., Gur, R.C., Moser, E., Habel, U., 2008b. Facial emotion recognition and amygdala activation are associated with menstrual cycle phase. *Psychoneuroendocrinology* 33 (8), 1031–1040.
- Dreher, J.C., Schmidt, P.J., Kohn, P., Furman, D., Rubinov, D., Berman, K.F., 2007. Menstrual cycle phase modulates reward-related neural function in women. *Proc. Natl. Acad. Sci.* 104, 2465–2470.
- Farage, M.A., Osborn, T.W., MacLean, A.B., 2008. Cognitive, sensory, and emotional changes associated with the menstrual cycle: a review. *Arch. Gynecol. Obstet.* 278 (4), 299–307.
- Fessler, D.M.T., 2001. Luteal phase immunosuppression and meat eating. *Biol. Forum* 94 (3), 403–426.
- Fessler, D.M.T., 2002. Reproductive immunosuppression and diet. *Curr. Anthropol.* 43, 19–61.
- Fessler, D.M.T., Navarrete, C.D., 2003. Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evol. Hum. Behav.* 24 (6), 406–417.
- Flaxman, S.M., Sherman, P.W., 2000. Morning sickness: a mechanism for protecting mother and embryo. *Q. Rev. Biol.* 75 (2), 113–148.
- Fleischman, D.S., Fessler, D.M.T., 2011. Progesterone's effects on the psychology of disease avoidance: support for the compensatory behavioral prophylaxis hypothesis. *Horm. Behav.* 59, 271–275.
- Franchimont, P., Dourcy, C., Legros, J.J., Reuter, A., Vrindts-Gevaert, Y., Van Cauwenberge, J.R., Gaspard, U., 1976. Prolactin levels during the menstrual cycle. *Clin. Endocrinol. (Oxf.)* 5 (6), 643–650.
- Frank, T.C., Kim, G.L., Krzemien, A., Van Vugt, D.A., 2010. Effect of menstrual cycle phase on cortic limbic brain activation by visual food cues. *Brain Res.* 1363, 81–92.
- Goldstein, J.M., 2005. Hormonal cycle modulates arousal circuitry in women using functional magnetic resonance imaging. *J. Neurosci.* 25 (40), 9309–9316.
- Guapo, V.G., Graeff, F.G., Zani, A.C.T., Labate, C.M., dos Reis, R.M., Del-Ben, C.M., 2009. Effects of sex hormonal levels and phases of the menstrual cycle in the processing of emotional faces. *Psychoneuroendocrinology* 34 (7), 1087–1094.
- Hahn, A.C., DeBruine, L.M., Fisher, C.I., Jones, B.C., 2015. The reward value of infant facial cuteness tracks within-subject changes in women's salivary testosterone. *Horm. Behav.* 67, 54–59.
- Halbreich, U., Borenstein, J., Pearlstein, T., Kahn, L.S., 2003. The prevalence, impairment, impact, and burden of premenstrual dysphoric disorder (PMS/PMDD). *Psychoneuroendocrinology* 28, 1–23.
- Humphrey, K., Underwood, G., Lambert, T., 2012. Salience of the lambs: a test of the saliency map hypothesis with pictures of emotive objects. *J. Vis.* 12, 1–15.
- Jones, B.C., Little, A.C., Boothroyd, L., DeBruine, L.M., Feinberg, D.R., Smith, M.J.L., Cornwell, R.E., Moore, F.R., Perrett, D.I., 2005a. Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm. Behav.* 48 (3), 283–290.
- Jones, B.C., Perrett, D.I., Little, A.C., Boothroyd, L., Cornwell, R.E., Feinberg, D.R., Tiddeman, B.P., Whiten, S., Pitman, R.M., Hillier, S.G., Burt, D.M., Smith, M.R., Smith, M.J.L., Moore, F.R., 2005b. Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proc. R. Soc. B: Biol. Sci.* 272 (1561), 347–354.
- Kottler, M.L., Coussieu, C., Valensi, P., Levi, F., Degrelle, H., 1989. Ultradian, circadian and seasonal variations of plasma progesterone and LH concentrations during the luteal phase. *Chronobiol. Int.* 6 (3), 267–277.
- Kumari, V., Corr, P.J., 1998. Trait anxiety, stress and the menstrual cycle: effects on Raven's Standard Progressive Matrices test. *Pers. Individ. Differ.* 24 (5), 615–623.
- Kuniecki, M., Wołoszyn, K., Domagalik, A., Pilarczyk, J., 2018. Disentangling brain activity related to the processing of emotional visual information and emotional arousal. *Brain Struct. Funct.* 223 (4), 1589–1597.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2005. International Affective Picture System (IAPS): Affective Ratings of Pictures and Instruction Manual (Technical Report A-8). University of Florida, Gainesville, FL.
- Lisofsky, N., Lindenberger, U., Kühn, S., 2015. Amygdala/hippocampal activation during the menstrual cycle: evidence for lateralization of effects across different tasks. *Neuropsychology* 67, 55–62.
- Little, A.C., 2013. The influence of steroid sex hormones on the cognitive and emotional processing of visual stimuli in humans. *Front. Neuroendocr.* 34 (4), 315–328.
- Lorenz, K., 1943. Die angeborenen Formen möglicher Erfahrung [The innate forms of potential experience]. *Z. Tierpsychol.* 5, 233–519.
- Luck, S.J., Woodman, G.F., Vogel, E.K., 2000. Event-related potential studies of attention. *Trends Cogn. Sci.* 4, 432–440.
- Maner, J.K., Miller, S.L., 2013. Hormones and social monitoring: menstrual cycle shifts in progesterone underlie women's sensitivity to social information. *Evol. Hum. Behav.* 35 (1), 9–16.
- Marchewka, A., Żurawski, L., Jednoróg, K., Grabowska, A., 2014. The Nencki Affective Picture System (NAPS): introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behav. Res. Methods* 46 (2), 596–610.
- Masataka, N., Shibasaki, M., 2012. Premenstrual enhancement of snake detection in visual search in healthy women. *Sci. Rep.* 2, 1–4.
- Nielsen, S.E., Ahmed, I., Cahill, L., 2013. Sex and menstrual cycle phase at encoding influence emotional memory for gist and detail. *Neurobiol. Learn. Mem.* 106, 56–65.
- Nummenmaa, L., Hyönä, J., Calvo, M.G., 2009. Emotional scene content drives the saccade generation system reflexively. *J. Exp. Psychol. Hum. Percept. Perform.* 35 (2), 305–323.
- Ossewaarde, L., Hermans, E.J., van Wingen, G.A., Kooijman, S.C., Johansson, I.M., Bäckström, T., Fernández, G., 2010. Neural mechanisms underlying changes in stress-sensitivity across the menstrual cycle. *Psychoneuroendocrinology* 35 (1), 47–55.
- Osterlund, M.K., Hurd, Y.L., 2001. Estrogen receptors in the human forebrain and the relation to neuropsychiatric disorders. *Prog. Neurobiol.* 64, 251–267.
- Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a “low road” to “many roads” of evaluating biological significance. *Nat. Rev. Neurosci.* 11 (11), 773–783.
- Phelps, E.A., LeDoux, J.E., Place, W., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron* 48, 175–187.
- Pilarczyk, J., Kuniecki, M., 2014. Emotional content of an image attracts attention more than visually salient features in various signal-to-noise ratio conditions. *J. Vis.* 14, 1–19.
- Pletzer, B., Petasis, O., Cahill, L., 2014. Switching between forest and trees: opposite relationship of progesterone and testosterone to global-local processing. *Horm. Behav.* 66 (2), 257–266.
- Pourtois, G., Schettino, A., Vuilleumier, P., 2013. Brain mechanisms for emotional influences on perception and attention: what is magic and what is not. *Biol. Psychol.* 92 (3), 492–512.
- Protopopescu, X., Pan, H., Altemus, M., Tuescher, O., Polanecsky, M., McEwen, B., Silbersweig, D., Stern, E., 2005. Orbitofrontal cortex activity related to emotional processing changes across the menstrual cycle. *Proc. Natl. Acad. Sci. U. S. A.* 102 (44), 16060–16065.
- Rilling, J.K., 2013. The neural and hormonal bases of human parental care. *Neuropsychology* 51 (4), 731–747.
- Robinson, D.P., Klein, S.L., 2012. Pregnancy and pregnancy-associated hormones alter immune responses and disease pathogenesis. *Horm. Behav.* 62, 263–271.
- Rupp, H.A., Wallen, K., 2007a. Relationship between testosterone and interest in sexual stimuli: the effect of experience. *Horm. Behav.* 52 (5), 581–589.
- Rupp, H.A., Wallen, K., 2007b. Sex differences in viewing sexual stimuli: an eye-tracking study in men and women. *Horm. Behav.* 51, 524–533.
- Sabatini, D., Flaisch, C.A.T., Bradley, M.M., Fitzsimmons, J.R., Lang, P.J., 2006. Affective picture perception: gender differences in visual cortex? *Neuroreport* 15 (7), 1109–1112.
- Salonia, A., Nappi, R.E., Pontillo, M., Daverio, R., Smeraldi, A., Briganti, A., Fabbri, F., Zanni, G., Rigatti, P., Montorsi, F., 2005. Menstrual cycle-related changes in plasma oxytocin are relevant to normal sexual function in healthy women. *Horm. Behav.* 47 (2), 164–169.
- Schupp, H.T., Junghöfer, M., Weike, A.I., Hamm, A.O., 2004. The selective processing of briefly presented affective pictures: an ERP analysis. *Psychophysiology* 41, 441–449.
- Sundström Poromaa, I., Gingnell, M., 2014. Menstrual cycle influence on cognitive function and emotion processing – from a reproductive perspective. *Front. Neurosci.* 8, 1–16.
- Syrop, C.H., Hammond, M.G., 1987. Diurnal variations in midluteal serum progesterone measurements. *Fertil. Steril.* 47 (1), 67–70.
- Tatler, B., 2007. The central fixation bias in scene viewing: selecting an optimal viewing position independently of motor biases and image feature distributions. *J. Vis.* 7 (14), 1–17.
- Tersman, Z., Collins, A., Eneroth, P., 1991. Cardiovascular responses to psychological and physiological stressors during the menstrual cycle. *Psychosom. Med.* 53 (2), 185–197.
- Toffoletto, S., Lanzemberger, R., Gingnell, M., Sundström Poromaa, I., Comasco, E., 2014. Emotional and cognitive functional imaging of estrogen and progesterone effects in the female human brain: a systematic review. *Psychoneuroendocrinology* 50, 2–52.
- van Hooff, J.C., Devue, C., Vieweg, P.E., Theeuwes, J., 2013. Disgust- and not fear-evoking images hold our attention. *Acta Psychol.* 143 (1), 1–6.
- van Hooff, J.C., van Buuringen, M., El M'rabet, I., de Gier, M., van Zalingen, L., 2014. Disgust-specific modulation of early attention processes. *Acta Psychol.* 152, 149–157.
- Wallen, K., Rupp, H.A., 2010. Women's interest in visual sexual stimuli varies with menstrual cycle phase at first exposure and predicts later interest. *Horm. Behav.* 57 (2), 263–268.
- Wolohan, F.D.A., Bennett, S.J.V., Crawford, T.J., 2013. Females and attention to eye gaze: effects of the menstrual cycle. *Exp. Brain Res.* 227 (3), 379–386.
- Zeidan, M.A., Igoe, S.A., Linnman, C., Vitalo, A., Levine, J.B., Klibanski, A., Goldstein, J.M., Milad, M.R., 2011. Estradiol modulates medial prefrontal cortex and amygdala activity during fear extinction in women and female rats. *Biol. Psychiatry* 70 (10), 920–927.