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Sex hormones predict the sensory strength and vividness of mental imagery

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ABSTRACT

Mystery has long surrounded the cause of large individual differences in mental imagery vividness and strength, and how these might map onto mental disorders. Here, we report that the concentration of sex hormones predicts the strength and vividness of an individual's visual mental imagery. We employed an objective measure of imagery utilizing binocular rivalry and a subjective questionnaire to assess imagery and how it relates to sex hormones. The strength and vividness of imagery was greater for females in the mid luteal phase than both females in the late follicular phase and males. Further, imagery strength and vividness were significantly correlated with salivary progesterone concentration. For the same participants, performance on visual and verbal working memory tasks was not predicted by progesterone concentration. These results suggest that sex hormones might selectively influence visual imagery, and not general cognitive abilities such as working memory. As hormone concentration changes over time, these data suggest a partial dynamic basis for individual differences in visual mental imagery, any dependent cognitive functions, and mental disorders.

Q4

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Mental images are formed when perceptual information is constructed from memory in the absence of relevant sensory input, giving rise to the experience of 'seeing with the mind's eye' (Kosslyn, Ganis, & Thompson, 2001). The ability to create, sustain and modify images in the mind plays a fundamental role in everyday behavior such as spatial navigation, episodic memory, working memory, making future predictions, language comprehension, creativity and even tests for consciousness (Just, Newman, Keller, McEleney, & Carpenter, 2004; Keogh & Pearson, 2011; LeBoutillier & Marks, 2003; Owen et al., 2006; Sack, 2005; Szpunar, Watson, & McDermott, 2007). Further, imagery is a major component of many psychopathologies and increasingly plays a role in their treatments (Holmes & Mathews, 2010; Holmes, Arntz, & Smucker, 2007).

One of the puzzling hallmarks of imagery is the large variance in strength and vividness from one individual to the next. Since the work of Sir Francis Galton (Galton, 1880) it has been known that individuals differ markedly in their self-reported imagery. However, over the years research has struggled to identify the cause of such individual variability. Highlighting one potentially promising avenue of inquiry, there is evidence that females generally have more vivid imagery than males (Campos & Perez, 1988).

Likewise, following a traumatic event, even when the types of trauma are controlled for, females are about twice as likely to develop PTSD compared to males (McLean & Anderson, 2009). Females report more intrusive mental images following a traumatic event than males (Ferree & Cahill, 2009) and females in the luteal phase (associated with elevated levels of sex hormones) experience more intrusive imagery (Ferree, Kamat, & Cahill, 2011) and display superior memory for emotion-laden events (Canli, Desmond, Zhao, & Gabrieli, 2002) than females in other phases of the menstrual cycle. In female humans and rats, research suggests that sex hormones can affect the processes of associative learning by modulating the effectiveness of extinction learning (Graham & Milad, 2013). In light of this, we sought to investigate the relationship between sex hormones and voluntary mental imagery, with the hypothesis that sex hormones might affect, or at least predict, imagery strength and vividness.

It has been demonstrated that estrogen is associated with activity in frontal and parietal areas during spatial memory tasks such

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as mental rotation tasks (Schöning et al., 2007), and it has been linked to verbal fluency (Maki, Rich, & Rosenbaum, 2002), while progesterone in women correlates positively with visual perception (Broverman et al., 1981; Wijayanto, Tochihara, Wijaya, & Hermawati, 2009). Estradiol (an estrogenic hormone) is known to decrease inhibitory gamma-aminobutyric acid (GABA), known to play important inhibitory role in sensory perception (Edden, Muthukumaraswamy, Freeman, & Singh, 2009; Rudick & Woolley, 2001; van Loon et al., 2013; Wallis & Luttge, 1980; Yoon et al., 2010). In addition, estradiol has direct excitatory effects on cell membranes, leading to a decrease in firing thresholds and an increase in mean resting state activity (Smith, 1989; Toran-Allerand et al., 2002; Wong & Moss, 1992). However, in many cases progesterone antagonizes estradiol actions and is thought to indirectly enhance the effects of GABA (Kokate, Svensson, & Rogawski, 1994; McEwen, 2001; Reddy, Castaneda, O'Malley, & Rogawski, 2004).

Hormone cycle-related fluctuations in cognition and perception are difficult to accurately assess in humans, due to the antagonistic influence of progesterone and its effects on neural, perceptual and cognitive functioning (Becker, 2005; Finocchi & Ferrari, 2011). Spikes in estradiol concentration can appear without co-occurring spikes in progesterone, but rises in progesterone are typically accompanied by high estradiol in the mid luteal phase of the menstrual cycle (Thorneycroft, Mishell, Stone, Kharma, & Nakamura, 1972). In addition, many human studies suffer from a reliance on self-report of menstrual stage, which may limit the reliability and accuracy of menstrual categorisation (Maki & Resnick, 2001; Sherwin, 2005).

The present study investigated the role of sex hormones in the individual differences in imagery strength by measuring levels of progesterone and 17β-estradiol (the predominant estrogenic hormone during reproductive years) and relating this to performance on objective and subjective indices of imagery strength and vividness. Recognizing that the processes of visual imagery and visual working memory overlap (Baddeley & Andrade, 2000; Keogh & Pearson, 2011, 2014), we also controlled for visual and verbal working memory. We hypothesized that imagery would be strongest in females in the luteal phase of the menstrual cycle because both estrogen and progesterone are elevated in the luteal phase, and both of these hormones have been linked to enhanced performance on perceptual tasks.

1. Method

1.1. Participants

Fifty-five participants (20 males, 19 follicular females, 16 mid luteal females; mean age 20.87 years, $SD = 2.90$) participated in experiment 1, and sixty-four participants (24 males, 20 late follicular females, 20 mid luteal females; mean age 20.16 years, $SD = 3.10$) participated in experiment 2. These numbers were decided prior to data collection and were based on previous experiments and investigations into mental imagery. All participants were recruited from an undergraduate psychology course and were given course credit in return for participation. All females were naturally cycling (i.e. not taking oral or other forms of contraceptive), and not experiencing any menstrual or hormonal abnormalities (e.g. endometriosis, or cycles less than 24 or greater than 32 days in length). Female participants in experiment 1 were assigned to either the follicular (1–14 days post menstruation) or mid luteal group (18–24 days post menstruation), and in experiment 2 the late follicular (8–13 days post menstruation) or the mid luteal group, based on their position in the cycle when they scheduled participation. Participants were scheduled for experimental sessions by counting forward the appropriate number of days from the next onset of menstruation. In experiment 2 this assignment was confirmed using salivary progesterone concentration. In some cases, difficulties were experienced in calibrating the binocular rivalry stimulus to compensate for eye dominance, and consequently six participants did not complete the binocular rivalry task.

1.2. Materials

To obtain a subjective self-report measure of visual imagery in both experiments, we administered the Vividness of Visual Imagery Questionnaire 2 (Marks, 1973, 1995). This task requires participants to create a visual image in their mind and then provide ratings of the vividness of the image.

Understanding the mechanisms of imagery has been partly limited by the lack of objective and reliable means to measure imagery. Recent behavioral and neural imaging research suggests that imagery can be studied objectively (Kosslyn et al., 2001; Naselaris, Olman, Stansbury, Ugurbil, & Gallant, 2015; Pearson, Clifford, & Tong, 2008; Pearson, Rademaker, & Tong, 2011; Stokes, Thompson, Cusack, & Duncan, 2009; Tartaglia, Bamert, Mast, & Herzog, 2009). Pearson et al. (2008) developed an objective measure for assessing visual mental imagery strength, utilizing brief presentations of binocular rivalry, a sensory phenomenon in which each eye is presented with a different pattern, causing them to compete for perceptual dominance (Blake & Logothetis, 2002; Pearson & Brascamp, 2008). In this task, participants are instructed to create a mental image of a specific stimulus, and the effect of that mental image on the perception of a subsequent binocular rivalry stimulus is taken as a measure of sensory imagery strength. Prior imagery of one of the patterns used in the rivalry stimulus can increase the probability that the pattern will achieve perceptual dominance during a brief rivalry presentation. This behavioral measure is perceptual in nature, is independent of response bias (Keogh & Pearson, 2011; Pearson, 2014; Pearson et al., 2008, 2011; Rademaker & Pearson, 2012), is reliable (Rademaker & Pearson, 2012), and has demonstrated that imagery conforms to the known characteristics of early visual cortex, which are unknown to naïve participants (Chang, Lewis, & Pearson, 2013; Pearson et al., 2008). Research using this method has also shown that imagery can be dissociated from visual attention (Pearson et al., 2008) and is predicted by the vividness of individual episodes of imagery, on a trial-by-trial basis (Pearson et al., 2011).

The binocular rivalry method was utilized as an objective measure of individual differences in the sensory strength of imagery in experiment 2. The rivalry stimulus was composed of two different Gabor patterns – a red horizontal Gabor pattern presented to the right eye, and a green vertical Gabor pattern presented to the left (both 1 cycle/°, Gaussian $\sigma = 4.5°$). This was achieved with the aid of red/green anaglyph glasses. The spatial phase of each grating was randomized on each presentation. Commission Internationale de l'Eclairage color values of the stimuli were as follows – green: $x = 0.293$, $y = 0.572$; red: $x = 0.602$, $y = 0.353$. Maximum luminance of the patterns was 11 cd/m^2. All stimuli were generated in Windows 7 using MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) on an Alienware LCD monitor (resolution of 1920 × 1080 pixels, 60 Hz refresh rate). A chinrest was secured to the desk to standardize viewing position at 57 cm from the monitor. Imagery, visual and number working memory tasks were conducted in a windowless room with almost no ambient light.

We were also able to test for demand characteristics and decisional bias in this task. On catch trials, a perceptually stable rivalry imitation stimulus was presented to both eyes, and hence it was not possible for imagery to affect the perception of the non-ambiguous mock rivalry stimulus at a supra-threshold level. The mock stimuli consisted of equal parts of each color, thus the correct response expected from a subject was the "mixed" key. Any bias to report the mock stimuli as unitary (e.g., red – same as imagery) suggested a criterion or decisional bias. Catch trials were interspersed randomly among rivalry trials to allow for the detection of any decisional biases. These scores were determined by calculating the percentage of trials on which a participant's response was biased in favor of the imagined Gabor pattern. In total, there were 30 rivalry trials and 10 catch trials.

The visual working memory task employed a stimulus consisting of a set of 2–6 greyscale Gabor patterns (1.43 cycles/°, Gaussian $\sigma = 1.25°$) presented at varying orientations, arranged in a circular fashion around a central fixation point with a 10° diameter. The stimulus for the verbal/number working memory task was a string of 6–11 numbers, and the numbers themselves ranged from 1 to 10.

1.3. Procedure

In experiment 1, participants signed a consent form and then completed the VVIQ2 (Marks, 1973, 1995). In experiment 2, participants provided written consent and completed the VVIQ2. To minimize potential effects of eye dominance in the binocular rivalry task it was necessary to first adjust the relative strength of the Gabor patterns using a simple perceptual task (Keogh & Pearson, 2011; Pearson et al., 2008, 2011; Rademaker & Pearson, 2012; Sherwood

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& Pearson, 2010). The output from this task was used to calibrate the rivalry stimulus for the subsequent imagery task.

The binocular rivalry task was then administered (see Fig. 1A for a timeline of a single trial). The binocular rivalry method requires participants to imagine the Gabor pattern indicated by a letter cue displayed for 1 s at the beginning of each trial, with 'R' corresponding to the red horizontal Gabor pattern and 'G' corresponding to the green vertical Gabor pattern. It was explained that participants should imagine (i.e. mentally visualize) the cued stimulus as though it were actually displayed on the monitor as best they could. Following this the screen went blank (except for the fixation point) for 5 s while participants imagined the stimulus. The rivalry stimulus was then presented for 0.75 s, and participants were required to indicate which of the two patterns appeared dominant, or if they appeared equally mixed. There was a 1 s gap between trials. The measure of mental imagery was taken as the percentage of trials on which the dominant pattern matched the one previously imagined. Thus, the extent to which this bias deviated from chance (50%) represented individual imagery strength. After a 5 min break, participants rinsed their mouths to remove food particles that could potentially contaminate the saliva sample, and then drooled or spat into a polystyrene tube. The sample was frozen at −20 °C until analyses were conducted.

Participants then completed the two working memory tasks; one assessed visual working memory and the other assessed verbal/number working memory. The order of these tasks was counterbalanced across participants. In each trial of the visual working memory task, the array of Gabor patterns was displayed for 1 s, after which the screen went blank for 6 s and participants were required to remember the orientation of each of the patterns in that set. One of the patterns from the original set was then displayed alone, in the same location but rotated ±20°. The stimulus remained on screen until the participant pressed a key to indicate which direction (clockwise or anticlockwise) the single pattern had been rotated. Fig. 1B shows the timeline of a visual working memory trial. There were six trials for each of the five set sizes, resulting in a total of 30 trials.

Fig. 1C shows the timeline of a number working memory task trial. The number string was presented on screen for 2 s, after which the screen went blank for 6 s and participants were required to remember the numbers for this period. Two number strings were then displayed one after the other for 2 s each, one of which was identical to the original string and another which differed by a single number. After presentation of both strings, participants indicated which of the two strings was identical to the original. There were 6 trials for each set size, for a total of 36 trials.

Note that some other tasks were run in this session, for more details please see authors note at the end of paper or see (Wassell, Rogers, Felmingam, Pearson, & Bryant, 2015).

1.4. Additional information about hormone analyses

Salivary 17-estradiol and salivary progesterone were collected via 1 mL passive drool into an enzyme immunoassay kit and were immediately frozen at −20 °C. Samples were stored at this temperature until assayed by Stratech Scientific, Sydney, Australia. On the day of assay appropriate number of samples were thawed for determination using commercially available ELISA kits (Salimetrics, USA) according to the manufacturers instructions. Thawed samples were centrifuged at 1500 × *g* for 15 min to collect clear saliva and this saliva was used without further processing for all assays. All samples were brought to room temperature before adding to assay wells and samples were analyzed in duplicate.

The intra-assay error of salivary progesterone was 4.5% and inter-assay variability was 5.1%, with assay sensitivity (the minimal concentration that can be distinguished from zero) of 5.0 pg/mL. The intra-assay error of salivary estradiol was 5.8% and inter-assay variability was 6.6%, with assay sensitivity equal to 0.1 pg/mL. According to Schultheis and Stanton (2009), precision estimates of intra- and inter-assays less than 10% are considered good. Calibrator ranges (i.e. usable detection range) for estradiol was 1–32 pg/mL, and for progesterone, 10–2430 pg/mL. Recovery for estradiol and progesterone samples ranged between 101% and 109%.

2. Results

2.1. Experiment 1

In experiment 1 participants filled in the VVIQ2 and reported their current menstrual phase by counting backward the appropriate number of days from the next onset of menstruation. We grouped female participants according to these reports. Fig. 2A shows the mean VVIQ2 score for males and females in the follicular and mid luteal phases (males: $M = 56.60$, $SD = 10.39$, follicular women: $M = 60.11$, $SD = 8.84$, mid luteal women: $M = 69.38$, $SD = 8.52$). VVIQ2 scores varied between menstrual groups, as confirmed by a significant one-way ANOVA, $F(2, 52) = 8.63$, $p < .001$, $\eta^2 = .25$. Tukey post hoc comparisons revealed that mid luteal females reported more vivid imagery than males, $p < .001$, $d = 1.34$, and follicular females, $p < .05$, $d = 1.07$, while males and follicular females did not differ, $p = .48$, $d = 0.37$. These data suggest a possible link between sex hormone concentration and the vividness of mental imagery.

2.2. Experiment 2

In light of the data from experiment 1, experiment 2 again measured imagery vividness using the VVIQ2, but also assessed sensory imagery strength using the objective binocular rivalry method (Fig. 1A). Rather than rely on self-report menstrual phase, here we also measured sex hormone concentration for each participant. See Table 1 for participant characteristics, indexes of imagery, and working memory measures.

2.3. Hormone analyses

Significant skewness and kurtosis were detected in the salivary data. Square root transformed values were used in all subsequent analyses to correct for this (although absolute values are reported for means and standard deviations).

Salivary estradiol ranged from a minimum of 1.41 pg/mL to a maximum of 9.02 pg/mL, with a mean of 3.76 pg/mL, standard deviation of 1.84 pg/mL, and variance of 3.40 pg/mL. Salivary progesterone ranged from 3.74 pg/mL to 530.60 pg/mL, with a mean of 127.80 pg/mL, standard deviation of 123.80 pg/mL, and a variance of 15325.42 pg/mL.

Progesterone concentration differed significantly between the three menstrual groups, $F(2, 61) = 7.46$, $p < .01$, $\eta^2 = .20$. Mid luteal females exhibited higher progesterone levels relative to late follicular females, $p < .01$, $d = 1.06$, and males, $p < .01$, $d = 0.98$. Estradiol concentrations were not significantly different between the menstrual groups, $F(2, 61) = 0.90$, $p = .41$, $\eta^2 = .03$. This result indicates that females' reports of their position in the menstrual cycle was valid, as mid luteal females' progesterone concentrations were expected to be higher than those of late follicular females, however estradiol did not predict the reported phases.

2.4. Mental imagery across menstrual phase

Fig. 2B shows the VVIQ2 data from Experiment 2. This pattern of results replicates those found in experiment 1, $F(2,61) = 7.35$, $p < .01$,

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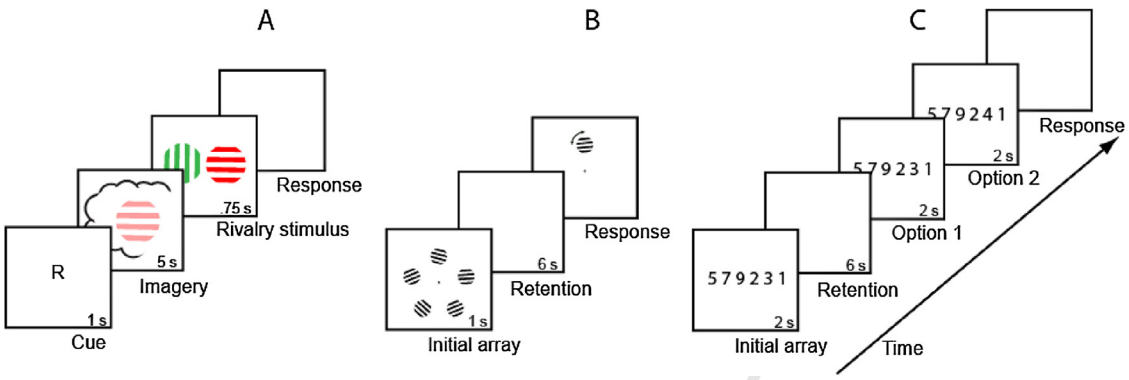

Fig. 1. Timelines for the three behavioral tasks. (A) Binocular rivalry imagery task, (B) visual working memory task, and (C) number working memory task.

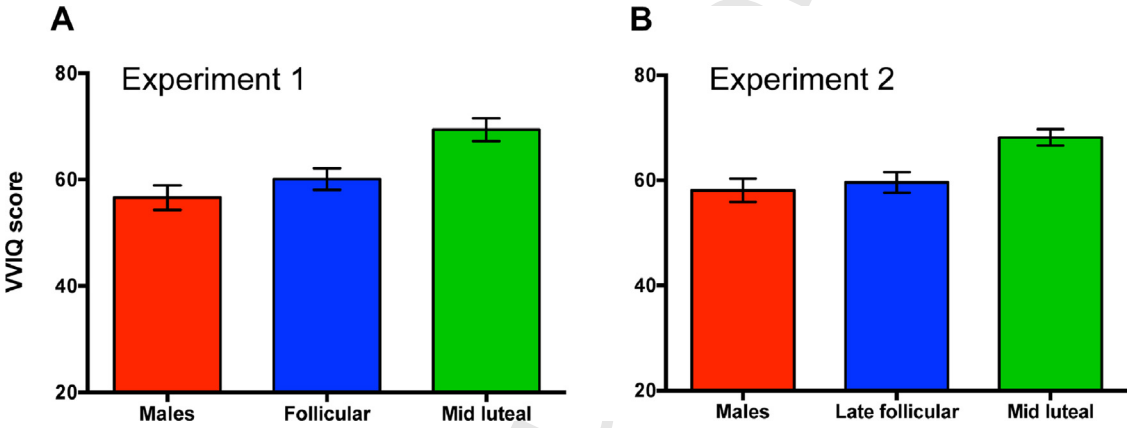

Fig. 2. VVIQ2 scores by self-report menstrual group for (A) data from experiment 1. (B) Data from experiment 2, an independent group. Error bars show ± SEM.

$\eta^2 = .19$, as mid luteal females scored higher than males, $p < .01$, $d = 1.10$, and late follicular females, $p < .05$, $d = 1.08$, while males and late follicular females did not differ in their scores, $p = .85$, $d = 0.15$.

VVIQ2 scores were found to significantly correlate with imagery strength from the binocular rivalry task, $r = .37$, $p < .01$. As is evident in Fig. 3A, imagery strength measured by the binocular rivalry task varied significantly between menstrual groups, $F(2, 55) = 8.58$, $p < .001$, $\eta^2 = .24$, with mid luteal females showing stronger imagery than both males, $p < .05$, $d = 1.03$, and late follicular females, $p < .001$, $d = 1.26$. These latter two groups' scores did not differ significantly, $p = .51$, $d = 0.34$. Together, these findings support the questionnaire data, and the proposal that imagery differences are influenced by menstrual phase and sex hormone concentration.

Fig. 3B shows a significant positive correlation between VVIQ2 scores and salivary progesterone concentration (black dashed line, all participants: $r = .46$, $p < .001$; green plot, mid luteal: $r = .49$, $p < .05$; blue plot, late follicular: $r = .49$, $p < .05$; red plot, males: $r = .16$, $p = .41$). A similar positive correlation was found between salivary progesterone and imagery strength as measured with the binocular rivalry task (black dashed line, all participants: $r = .30$, $p < .05$; green plot, mid luteal: $r = .49$, $p < .05$; blue plot, late follicular: $r = -.10$, $p = .68$; red plot, males: $r = -.09$, $p = .72$; see Fig. 3C). This suggests that the individual differences in both self-reported imagery vividness and objective indices of imagery strength are associated with progesterone concentration.

The correlations between estradiol and VVIQ2 scores did not reach significance when including all participants, $r = .01$, $p = .97$, nor when broken down by menstrual group, mid luteal: $r = .02$, $p = .93$, late follicular: $r = -.09$, $p = .71$, males; $r = -.06$, $p = .79$. When calculated for all participants, the relationship between estradiol and imagery strength on the binocular rivalry task was not significant, $r = -.21$, $p = .12$. There was a significant negative correlation

Table 1
Mean participant characteristics from experiment 2.

	Males $N = 24$	Late follicular $N = 20$	Mid luteal $N = 20$
Age	19.63 (2.10)	20.25 (2.55)	20.70 (4.39)
Progesterone (pg/mL)	96.10 (116.77)	90.37 (71.77)	203.26 (142.89)
Estradiol (pg/mL)	3.44 (1.90)	3.95 (1.60)	3.97 (2.03)
VVIQ2	58.08 (10.92)	59.60 (8.75)	68.15 (6.97)
Imagery			
% Primed	64.57 (12.82)	59.69 (15.85)	77.48 (12.16)
Catch trials	51.02 (7.72)	49.72 (5.66)	53.43 (5.98)
Visual working memory	68.75 (23.73)	54.17 (25.86)	70.00 (15.86)
Verbal working memory	69.91 (13.70)	67.50 (15.22)	68.33 (12.37)

Note. Standard deviations appear in parentheses. Index of visual working memory is the percentage of correct responses to set size 3, index of verbal working memory is performance averaged across all set sizes.

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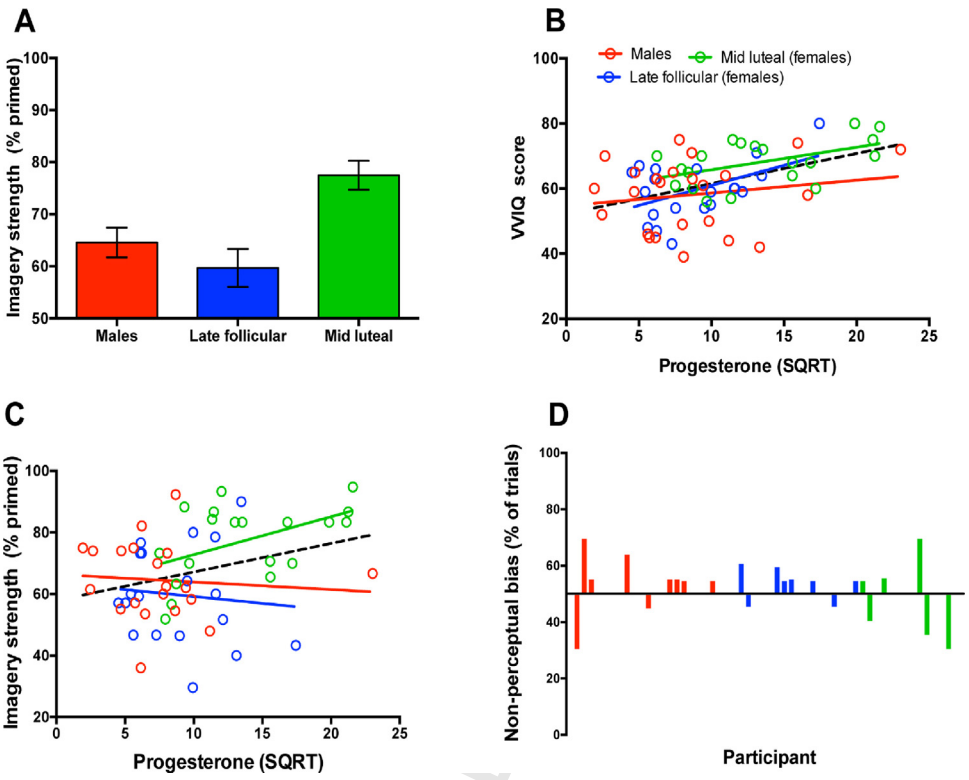

Fig. 3. Perceptual measures of mental imagery. **A.** Imagery strength (measured by binocular rivalry), female participants separated by self-reported menstrual group, error bars show ±SEM. (B) Relationship between salivary progesterone and VVIQ2 score in study 2. Color-coded the same as in (A) dashed black line shows the linear fit to the whole group. (C) Correlation between salivary progesterone and imagery strength (measured by binocular rivalry). (D) Catch trial response biases for each participant, color coded into the same 3 groups. Non-perceptual bias on the *Y*-axis, individual participants on the *X*-axis.

between estradiol and imagery strength for males, $r = -.52$, $p = .02$, however the relationship was not significant for mid luteal females, $r = -.41$, $p = .08$, or late follicular females, $r = .08$, $p = .76$.

Fig. 3D shows individual participants' mean non-perceptual bias on binocular rivalry catch trials; red bars correspond to male participants, blue to late follicular participants, and green to mid luteal participants. We analyzed this non-perceptual bias by coding veridical "mixed" responses to the catch trials (see methods) as 50%, while responses that matched the cued pattern were coded as 100, and responses opposite to the cued grating were coded as 0. Confirming that the imagery strength measure using binocular rivalry reflected individual imagery strength rather than any decisional biases or demand characteristics, the mean percentage of bias on catch trials was 51.41%, which was not significantly different to 50%, $t(51) = 1.53$, $p = .13$. Further, there were no significant differences in catch trial scores between menstrual groups, $F(2, 49) = 1.36$, $p = .27$, $\eta^2 = .05$.

2.5. Working memory

To assess visual working memory we utilized a two-alternative forced choice memory task in which participants had to hold multiple Gabor patterns in working memory for 6 s (see Fig. 1B). Fig. 4A shows the mean accuracy across set-sizes for the three menstrual groups on the visual working memory task. Our data agrees with previous literature that suggests sharp drop-offs in accuracy for visual working memory between set sizes 3 and 4 (Luck & Vogel, 1997; Schöning et al., 2007), and this is the set size at which working memory fidelity reaches asymptote (Anderson, Vogel, & Awh, 2011; Brady, Konkle, Gill, Oliva, & Alvarez, 2013; Zhang & Luck, 2008). In the present study, set size 3 showed the largest individual variance. For set size 3 there was a main effect of menstrual group, $F(2, 61) = 3.18$, $p < .05$, $\eta^2 = .09$., though none of the post hoc comparisons were significant (males vs. late follicular females, $p = .09$, $d = 0.59$, males vs. mid luteal females, $p = .98$, $d = 0.06$, mid luteal females vs. late follicular females, $p = .07$, $d = 0.74$).

Fig. 4C shows a scatter plot of visual working memory accuracy versus salivary progesterone concentration; the dashed black line is the line of best fit for all participants. Salivary progesterone did not significantly correlate with visual working memory at any individual set size (all $ps > 24$), nor did estradiol (all $ps > .31$). Replicating previous research (Keogh & Pearson, 2011, 2014), a marginally significant correlation was detected between imagery strength and visual working memory, $r = 26$, $p = .05$. These data suggest that even though imagery and visual working memory might overlap in mechanisms, progesterone concentration only predicts individual imagery strength, not visual working memory performance.

In contrast to the visual working memory data, no particular set size appeared to differentiate menstrual groups' performance on the verbal/number working memory task more than any other, as variances were comparable across all six set sizes (see Fig. 4B). Thus, the measure of verbal/number working memory used in statistical analyses was an average score for set sizes 8, 9 and 10 for each participant. There was no significant difference between menstrual groups when using this index of verbal/number working memory, $F(2, 61) = 0.17$, $p = .84$, $\eta^2 = .006$.

Fig. 4D shows the absence of a relationship between mean verbal working memory performance and progesterone concentration. The relationship between progesterone and verbal/number working memory was not significant when calculated for all participants, $r = .09$, $p = .48$, nor when calculated separately for males, $r = .04$, $p = .87$, late follicular females, $r = .09$, $p = .70$, or mid luteal females, $r = .24$, $p = .32$. Similarly, no significant relationship was detected

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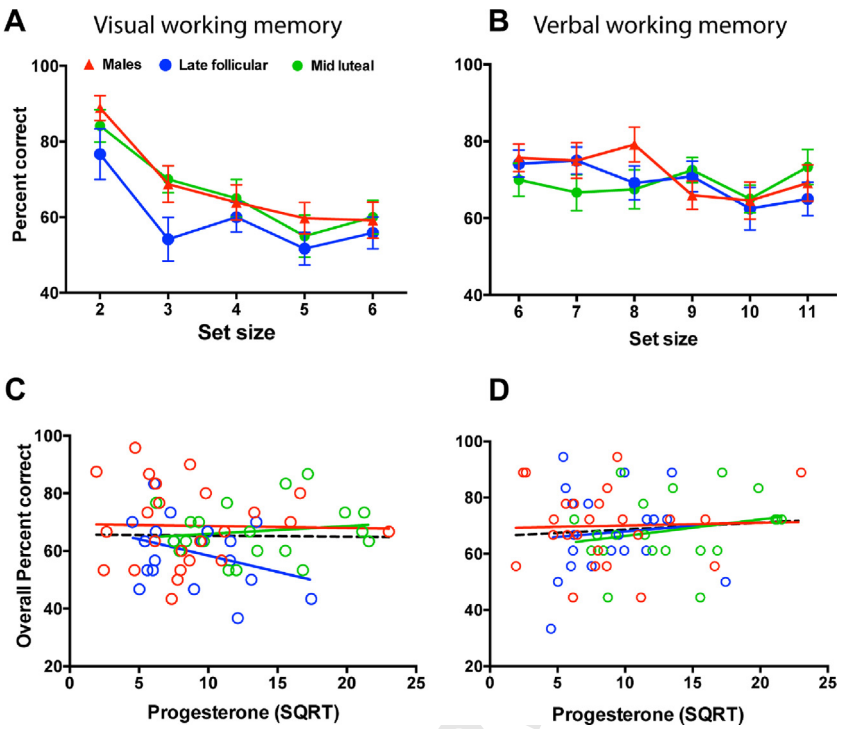

Fig. 4. Visual and verbal working memory scores coded by groups. (A) Visual working memory accuracy by menstrual group over the different set sizes. (B) Number working memory accuracy by menstrual group, over the different set sizes, all error bars show ±SEM. (C) Mean visual memory performance vs. progesterone concentration. (D) Mean verbal/numerical memory performance vs. progesterone concentration.

between estradiol and verbal/number working memory when including all participants, $r = -.17$, $p = .19$, or when only including males, $r = -.23$, $p = .28$, late follicular females, $r = .01$, $p = .98$, or mid luteal females, $r = -.23$, $p = .34$.

2.6. Imagery predictors

A simultaneous linear regression analysis on imagery strength (using the sensory strength of imagery) was performed, including progesterone, estradiol, visual working memory (set size 3), and verbal/number working memory (average scores for sets 8, 9, and 10) as predictors. The regression model explained a significant amount of the variance in imagery strength, $F(4, 53) = 5.86$, $p < .001$, $R^2 = .31$, $R^2_{adjusted} = .25$. Progesterone concentration was predictive of imagery, $R^2_{adjusted} = .42$, $p < .01$, as was estradiol, $R^2_{adjusted} = -.30$, $p < .05$, and visual working memory, $R^2_{adjusted} = .25$, $p < .05$.

3. Discussion

Here we provide evidence from two separate participant samples (experiment 1 and 2) that visual mental imagery (sensory strength and vividness) is related to sex hormones/menstrual phase. Specifically, these results demonstrate that higher concentrations of progesterone are predictive of increased individual visual imagery strength and vividness, using both self-report and objective perceptual measures. The finding that progesterone was not associated with visual or verbal working memory performance suggests that progesterone does not influence these functions in the same way as it interacts with visual imagery strength and vividness. Together these results suggest that variance in imagery vividness and strength might be at least partially contingent on fluctuations in progesterone.

Prior work using the binocular rivalry technique to assess the sensory strength of mental imagery has provided strong evidence that it is the content of the actual mental image that is priming or facilitating subsequent rivalry and not a non-perceptual bias or visual attention (see Pearson, 2014) for a review of the this particular method). Because of these reasons and the lack of any observed correlation between progesterone and working memory, we are confident that the observed relationship between progesterone and both sensory and subjective imagery vividness genuinely represents imagery and not any reporting bias.

One potential explanation of our findings involves the hormonal modulation of top-down voluntary control mechanisms, as opposed to the modulation of processes in sensory areas. Voluntary mental imagery lacks the automaticity of visual perception, as it requires conscious, effortful control. As such, it may be that menstrual-related changes in imagery are a consequence of changes in voluntary control functions arising from fluctuations in ovarian hormone concentrations. The mid luteal phase is associated with enhanced sustained attention relative to other phases, which is reportedly related to endogenous levels of progesterone (Maki & Resnick, 2001; Sherwin, 2005; Solís-Ortiz & Corsi-Cabrera, 2008). As a consequence, concentration could be increased and the potential impact of distractions minimized. This enhanced focus of cognitive resources could facilitate deliberate imagery generation and maintenance, leading to increases in the vividness of imagery. However, if such a top-down mechanism was driving the differences we observed in imagery strength, it has to be specific to imagery, as we did not observe such differences in visual or verbal working memory.

An alternative explanation is that the concentration of sex hormones could modulate sensory activity in the early visual cortex, thus boosting the sensory strength and vividness of mental imagery. This hypothesis would also suggest that measures of visual perception would be predicted by the concentration of sex hormones. However, as the current datasets do not include a purely perceptual measure, we cannot eliminate the possibility that the relationship between imagery and hormones extends to visual sensory perception.

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One interesting implication of the current results is that the strength of an individual's visual imagery may not be entirely static, especially for females. This merits consideration when interpreting data influenced by the strength or vividness of visual mental imagery. We are not proposing that hormone levels dictate visual imagery strength entirely, as it is more likely that multiple factors contribute to imagery. If at least part of the variance in imagery strength is due to dynamic rather than static factors, it is worth conceptualizing imagery strength as a dynamic process that involves both trait and state factors.

These findings may have important implications for potential role of progesterone in the maintenance and treatment of psychological disorders characterized by intrusive and distressing mental imagery. PTSD is largely defined by uncontrollable intrusive mental images, and one of the primary frontline treatments also involves employing mental imagery in forms of CBT (Foa & Meadows, 1997; Harvey, Bryant, & Tarrier, 2003). Further, individual differences in imagery vividness have been shown to predict the amount of intrusive images following exposure to aversive stimuli (Morina, Leibold, & Ehring, 2013), and voluntary mental images can undergo associative learning (Lewis, O'Reilly, Khuu, & Pearson, 2013), a likely mechanism of PTSD (Rauch, Shin, & Phelps, 2006).

Females who experience trauma during the mid luteal phase are more likely to experience flashback memories relative to females experiencing trauma in other phases (Bryant et al., 2010). Given that women develop PTSD at more than twice the rate of men (Breslau, Davis, Andreski, Peterson, & Schultz, 1997), it is possible that cycling ovarian hormones in women may in part enhance imagery strength and subsequently increase vulnerability to intrusive images.

Although cognitive behavioral therapy that utilizes imagery has been recognized as the treatment of choice for many psychopathologies, including a range of anxiety disorders, current treatments only alleviate PTSD in approximately 60–70% of people (Foa & Meadows, 1997; Harvey et al., 2003). Mental imagery is commonly used during such treatments, for example in imagined exposure procedures (Hunt & Fenton, 2007) and imagery rescripting procedures (Holmes et al., 2007). Voluntary mental images can undergo associative learning (Lewis et al., 2013) and associative learning can also be modulated by sex hormones (Graham & Milad, 2013). If mental imagery and associative learning are stronger during the mid luteal phase in women, might this suggest a window in which the proposed mechanisms of cognitive behavioral therapy utilizing imagery might be more effective?

Together our data suggest a link between voluntary mental imagery and sex hormones in females. However, the exact causative relationship at present remains unknown. Future research could utilize hormonal supplements to tease apart this relationship. Such fundamental scientific work on the cause of the individual differences in mental imagery, especially that which explores dynamic processes like fluctuations in sex hormones, has the potential to offer a unique contribution to our understanding of and the treatment for mental disorders.

Authors note

A separate study was run in conjunction with the data presented in the current paper. This work has been published in a separate paper, full details of all additional tasks, some of which were run within the same sessions as those described in this paper can be seen here (Wassell et al., 2015). The two papers have different objectives, Wassell et al. (2015) investigated the role of emotional memory consolidation in models of anxiety disorders and progesterone levels. The extra task involved 'visual' and 'verbal' evaluation of neural and negative images and subjects came back in two later when their memory of the images was tested for the full details of this memory task see the paper (Wassell, J. et al. (2015). Progesterone and mental imagery interactively predict emotional memories. *Psychoneuroendocrinology*, *51*, 1–10.).

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