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Sex hormones predict the sensory strength and vividness of mental imagery

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ABSTRACT

Mystery surrounds the cause of large individual differences in mental imagery vividness and strength, and how these might map onto mental disorders. Here, we report the concentration of sex hormones predicts the strength and vividness of visual mental imagery. We employed an objective measure of imagery utilizing binocular rivalry and a subjective questionnaire to assess imagery. 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 sex hormones might influence visual imagery, but not general working memory. As hormone concentration changes over time, this implies a partial dynamic basis for individual differences in visual mental imagery, any dependent cognition and mental disorders.

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