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Progesterone and mental imagery interactively predict emotional memories

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Summary Different lines of research suggest that the consolidation of emotional memories is influenced by (a) endogenous levels of sex hormones, and (b) individual differences in the capacity to use vivid mental imagery. No studies to date have investigated how these factors may interact to influence declarative emotional memories. This study examined the interacting influence of progesterone and mental imagery strength on emotional memory consolidation. Twenty-four men, 20 women from the low progesterone (follicular) menstrual phase, and 20 women from the high progesterone (mid-luteal) phase of the cycle were assessed using an objective performance-based measure of mental imagery strength, and then shown a series of aversive and neutral images. Half of the images were accompanied by instructions to process sensory features, and the remaining half to process the conceptual characteristics of the images. Two days later, all participants returned for a surprise free recall memory test. The interaction of progesterone and mental imagery strength significantly predicted recall of visually processed, but not verbally processed, negative images. These data suggest that mental imagery strength may be one mechanism underlying the documented association between endogenous progesterone and enhanced emotional memory performance in the literature.

It is widely acknowledged that emotional arousal has an enhancing effect on lasting, declarative memory (Cahill and McGaugh, 1995, 1998; Anderson et al., 2006). A significant body of literature from both animal and human studies suggests that emotional arousal triggers the release of noradrenergic and glucocorticoid stress hormones, that promote the preferential encoding of arousing over neutral information (McGaugh, 2004). These adrenal hormones are thought to interact in the amygdala of the brain to facilitate memory formation via afferent projections to the hippocampus and related cortical areas (McGaugh and Roozendaal, 2002). Further, cognitive researchers have proposed that the high

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levels of arousal triggered during a stressful experience promote the processing of sensory information, at the cost of conceptual (or verbal) processing (Ehlers and Clark, 2000). The outcome is that memory for highly emotional events is poorly contextualized, and instead contains predominantly visual sensory features that can be easily triggered by similar perceptual cues. Supporting this proposal is evidence that self-reported levels of data-driven (i.e. sensory) processing are positively associated with intrusive memories following stressful laboratory (Halligan et al., 2002) and real-life traumatic (Halligan et al., 2003; Ehring et al., 2008) events.

Research has shown that females have better declarative memory for emotionally arousing events than males. Specifically, females recall emotional autobiographical events more quickly and with greater emotional intensity, accuracy and detail than males (Seidlitz and Diener, 1998; Pillemer et al., 2003). Analog studies have similarly highlighted females' superior memory for emotionally arousing stimuli relative to men (Canli et al., 2002; Payne et al., 2006). One possible reason for sex differences in emotional memory pertains to fluctuations in sex hormones across the menstrual phase in women, which may predispose an individual to a heightened encoding and/or consolidation of emotional memory. One study assessed whether there were differences in recall of emotional images between naturally cycling women who encoded the stimuli during hormonally distinct phases of their menstrual cycles (Ertman et al., 2011); the authors found that deliberate retrieval of emotional material after a one-week delay was stronger when encoding occurred during the luteal (days 15—31 after menstruation; high hormone) phase, relative to the follicular phase (days 0—14 post menstruation; low hormone). Further, regression analyses demonstrated that salivary progesterone levels at the time of encoding correlated positively with free recall of emotional, but not neutral, stimuli. Less is known about the impact of estrogen on emotional memory, where some evidence indicates that high levels of estrogen are associated with enhanced extinction of fear responding (Glover et al., 2012; Graham and Milad, 2013); this suggests that the interactive effects of progesterone and estrogen likely have opposite effects of the formation of fear-based memories.

The literature in human imaging offers further support that sex hormones modulate the arousal circuitry of the brain during the encoding and consolidation of emotional stimuli. Studies have found that the administration of synthetic progesterone (van Wingen et al., 2008), and the naturally high levels of progesterone observed during the mid-luteal phase (Andreano and Cahill, 2010), were associated with enhanced amygdala reactivity to arousing images, compared to neutral images. There is evidence that cortisol peaks during the luteal period (Kirschbaum et al., 1999). Further, the association between cortisol and recall of emotional memories has been observed in the midluteal but not other phases of the menstrual cycle (Andreano et al., 2008). Further, it has been reported that preferential recall of negative information is associated with elevated progesterone levels and stress-induced cortisol increases (Felmingham et al., 2012). Other studies have focused on intrusive memories (involuntary memories that occur after encoding of information), and found that women had more intrusive memories of an emotional film if they viewed it during the luteal phase relative to the non-luteal phase (Ferree and Cahill, 2009). Moreover, women who suffered traumatic events during the mid-luteal phase were almost five times more likely to experience flashback memories than non-luteal women (Bryant et al., 2011). Taken together, these findings suggest that the luteal phase is associated with facilitated encoding and/or consolidation of emotional memories, and this may be associated with elevated progesterone levels.

A second factor that may contribute to the consolidation of emotional memories concerns an individual's capacity to engage vivid mental imagery (Krans et al., 2009; Morina et al., 2013). Kosslyn (2005) proposed that individuals who are generally prone to experience vivid and lifelike imagery may engage in heightened perceptual processing an emotional event, leading to a greater consolidation of sensory information and consequently increasing their risk of developing image-based intrusions. In addition, retrieval of vivid, sensory-rich details from memory can activate many of the same neural regions recruited during actual perception (Ganis et al., 2004) and can cause a person to respond as if the trauma is actually happening again (i.e. 'flashbacks; Holmes and Mathews, 2010).

At present there is a paucity of research regarding the distinct processes involved in involuntary and declarative emotional memories, as stipulated by the 'dual representation' model of emotional memory formation (e.g. Dalgleish, 2004). Although one study has found a significant positive relationship intrusions and the strength of explicit emotional memories (Ferree and Cahill, 2009), this relationship is tentative at this time. To date, no studies have investigated whether general capacity for imagery is related to different types of emotional memories. Despite this lack of direct evidence, there is indirect evidence from traumatic memories observed in posttraumatic stress disorder (PTSD). One study found that more vivid imagery was associated with more frequent flashbacks following a motor vehicle accident (Bryant and Harvey, 1996), and another reported that participants with PTSD had reported more vivid visual imagery than participants who had recovered from PTSD and non-traumatized participants (Jelinek et al., 2010). Vietnam veterans with high PTSD scores rate their mental images as more vivid than veterans with low PTSD symptomatology (Stutman and Bliss, 1985), although others have since failed to replicate this finding (e.g. Karatzias et al., 2009). Further complexity is seen in findings from nonclinical studies that have found both positive (Morina et al., 2013) and negative (Krans et al., 2010) associations between mental imagery and intrusions.

The goal of this study was to explore the possibility that progesterone and mental imagery strength may *interact* in contributing to emotional memories. Extrapolating from evidence that emotional memories are associated with progesterone levels and also with mental imagery, we consider here whether greater encoding and/or consolidation of emotional memories may be due to the relationship between hormone-related influences and imagery ability. The current study addressed this issue by presenting participants with aversive and neutral stimuli, with specific instructions for processing the visual sensory features or conceptual characteristics of the images (Hariri et al., 2003). Recognizing that the association of imagery and emotional recall is limited to intrusive rather than intentionally retrieved memories, we tested the associations with both forms of emotional