



Sex differences in emotional memory consolidation: The effect of stress-induced salivary alpha-amylase and cortisol

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ABSTRACT

This study examined sex differences in the emotional memory consolidation, and the impact of stress-induced cortisol and salivary alpha amylase responses on emotional memory recall. Following baseline salivary measures, 39 healthy women and 41 men viewed 20 neutral and 20 negative arousing images, and then underwent either a cold pressor stress test or control condition, followed by further salivary measures. Participants returned two days later for a free recall test. The stress condition induced greater cortisol response, and negative images were better recalled than neutral. Whereas women displayed greater recall of negative images under stress than men, they recalled fewer negative images in the control condition. Stress-induced cortisol predicted recall of negative images in women, and neutral images in men. This suggests there is an enhanced consolidation of negative images under stress in women that may be a potential mechanism for the greater female prevalence for developing anxiety disorders.

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1. Introduction

An outstanding question in psychiatry is why women are particularly vulnerable to developing anxiety disorders. Epidemiologic studies show that women develop anxiety disorders such as Generalized Anxiety Disorder, Posttraumatic Stress Disorder (PTSD), Specific Phobia and Panic Disorder at twice the rate of men (Kessler et al., 2005). Recently, researchers have postulated that biological mechanisms may contribute to the female prevalence for anxiety (Cahill, 2006).

Many anxiety disorders (in particular PTSD) are characterized by intrusive images and distressing memories (Brewin et al., 2010). Recent theoretical models converge in proposing that visually processed memories are associated with greater arousal (Brewin et al., 2010), which may lead to greater memory consolidation and recall (McGaugh, 2004). A prevailing model of emotional memory suggests that high levels of stress hormones (noradrenaline and cortisol) released at the time of encoding result in an overconsolidation of emotional memories (McGaugh, 2004). Therefore, a potential biological mechanism underlying the female prevalence for anxiety disorders may be greater consolidation of emotional memories, leading to increased intrusive memories.

Empirical support for the memory modulation hypothesis arises from findings that emotional memories are recalled better than neutral memories (Anderson et al., 2006; McGaugh, 2004). Direct pharmacological manipulation of the noradrenergic system via post training amygdala infusions of noradrenergic agonists, antagonists and a combination of the two have provided compelling evidence for the role of the noradrenergic system in memory consolidation in both rats and humans (Cahill and Van Stegeren, 2003; LaBar, 2007; McGaugh, 2004; O'Carroll et al., 1999; Southwick et al., 2002). There is also compelling evidence for a role of glucocorticoids and their interaction with noradrenaline in mediating memory consolidation in rats and humans (Roosendaal et al., 2006; Kukulja et al., 2008).

Women have been found to have better recall of emotional memories than men (Bloise and Johnson, 2007; Davis, 1999; Canli et al., 2002). In line with the memory modulation hypothesis (McGaugh, 2004), there is also evidence to suggest that this enhanced ability for emotional memory is mediated by arousal in women. A recent study examined a biomarker of endogenous noradrenaline (salivary alpha amylase (sAA) in response to negative arousing images, and found that 21 of the 24 noradrenergic responders were women and that noradrenergic response was associated with greater negative memory recall (Segal and Cahill, 2009). Although this is initial evidence of a greater noradrenergic response in women, several other studies examining salivary alpha amylase to negative arousing images (but not emotional memory) have failed to find stress-induced sex differences (Takai et al., 2007; Van Stegeren et al., 2006, 2008), and baseline alpha amylase levels

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have been reported as higher in men (Van Stegeren et al., 2008). A potential reason for this inconsistency is variability in controlling for oral contraceptive use and menstrual phase in women (Van Stegeren et al., 2008). Although alpha amylase has been shown to increase emotional images and physical stressors (Van Stegeren et al., 2008), no studies have examined sex differences in alpha amylase response to physical stressors. Recent animal evidence in response to acute physical restraint stress reveals greater activation of locus coeruleus neurons (the main noradrenergic nucleus in the brain) in female rats compared to males (Curtis et al., 2006; Valentino et al., 2011), and there appear greater dendritic branches on locus coeruleus neurons in female rats (Bangasser et al., 2011). Consistently, a recent functional magnetic resonance imaging (fMRI) study reported greater activation in dorsal brainstem and midbrain regions (in regions containing ascending noradrenergic signals) in females following trauma compared to males (Felmingham et al., 2010). Therefore, further research is required to examine sex differences in noradrenergic (via salivary alpha amylase) response to stress in humans who are not taking oral contraceptives.

Studies of sex differences in the relationship of stress-induced cortisol and memory also yield inconsistent findings. Although greater cortisol response to acute stress has been found in men (Kirschbaum et al., 1999; Cornelisse et al., 2011), these studies failed to control for menstrual phase in women and did not control for oral contraceptive use. Position in the menstrual cycle has been shown to have a potent effect on cortisol response (Kirschbaum et al., 1999), and cortisol has been shown to affect memory retrieval in naturally cycling women, but not in those taking hormonal contraception (Kuhlmann and Wolf, 2005). When controlling for menstrual phase, recent evidence reveals an association between cortisol and recall of negative images in the mid-luteal phase of the menstrual cycle (which is associated with greater glucocorticoid release) but not the early or late follicular phases (Andreano et al., 2008).

In summary, there is preliminary evidence that women display greater noradrenergic responses to stress, and have greater emotional memory recall than men. There is also an association between glucocorticoid release in the mid-luteal phase of the menstrual cycle and emotional memory recall in women. Accordingly, the greater female prevalence for developing anxiety disorders may be at least partially explained by a greater release of stress hormones, and thus greater memory consolidation and recall of emotional memories. The aim of the current study was to test this hypothesis by comparing salivary alpha amylase and cortisol responses following a stressor (compared to a control condition) presented immediately after encoding negative and neutral images in a sample of naturally cycling women. It was predicted that women would have greater delayed recall of threat images (but not neutral) compared to men, and that this would be mediated by salivary alpha amylase and cortisol responses to stress.

2. Methods

2.1. Participants

80 healthy undergraduate psychology students (41 women, 39 men) were recruited for the study as part of course credit. Participants were aged 18–40 years, had no history of psychiatric disorders, substance abuse, or traumatic brain injury, and were not taking psychoactive medications. Female participants had no menstrual irregularities and were not taking hormonal contraceptives. Women and men were randomly assigned to a stress (Cold Pressor Stress Test (CPS) or control (warm water) condition. To control for menstrual phase in women, the menstrual position of each participant was determined by self-report and confirmed by salivary progesterone. Women in different menstrual phases (4 women in the midluteal in each condition) were allocated in equal numbers to the control and stress conditions. After complete description of the study, written informed consent was obtained.

2.2. Measures

2.2.1. Questionnaires

The Depression Anxiety and Stress Scales (Lovibond and Lovibond, 1995; DASS) provided a self-report of depressed and anxious mood on the day of testing.

2.2.2. Salivary

Endogenous noradrenergic activity was measured by salivary alpha-amylase (sAA; Nater and Rohleder, 2009). There has been evidence from pharmacological studies in humans and animals supporting sAA as a valid biomarker for endogenous noradrenergic activity, as noradrenergic agonists (yohimbine) and antagonists (propranolol) increase and decrease sAA respectively (see Nater and Rohleder (2009) for review). Several studies have reported a relationship between sAA and emotional memory recall (Segal and Cahill, 2009; Van Stegeren et al., 2008). This study adopted Segal and Cahill's (2009) methodology but in order to maximize the noradrenergic response to stress, we incorporated a stressor, the CPS, which is widely used and has been shown to elevate endogenous stress hormones (Lovallo, 1975). sAA responses were collected at baseline and immediately following the CPS. Salivary cortisol responses were collected at baseline and 15 min following the CPS, to obtain maximal levels of cortisol following the examples of Andreano and Cahill (2006). To avoid morning variations of cortisol and sAA, all testing sessions were conducted between 1 p.m. and 6 p.m. Participants were asked to refrain from food, nicotine, and caffeine for 4 h, and alcohol and excessive exercise for 24 h, prior to the study.

2.3. Procedure

At the first session of the experiment, participants were randomly assigned to the CPS or control condition. After 15 min of habituation to the testing environment, saliva samples were taken to measure baseline sAA and cortisol responses. Participants then viewed a series of images (20 highly arousing negative ("threat") and 20 neutral slides) selected from the International Affective Picture System (IAPS; Lang et al., 2008). Each IAPS image was presented for 5 s, and after each image, participants rated each image according to arousal and valence using standardized Self-Assessment Manikin procedures (Lang et al., 2008). Participants were instructed to attend to the image when it was on the screen.

Immediately after viewing the images, participants underwent the CPS or control condition, following procedures of Andreano and Cahill (2006). Participants in the CPS condition were asked to keep their hand immersed in a bucket of very cold (0 °C) water for 3 min. Participants in the control condition placed their hand in warm water for 3 min. sAA samples were taken immediately following the stress/control procedure and cortisol samples were taken 15 min after the stress/control procedure. Participants were then asked to return for a second testing session two days after their initial testing session.

At the second session, saliva samples were taken to assess basal level of sAA and cortisol. Participants then completed a surprise free-recall memory test of the images viewed two days earlier. Participants were instructed to write descriptions of any images from the previous testing session (Segal and Cahill, 2009), and were then prompted for additional details for each image.

2.4. Saliva data analysis

Saliva samples were acquired naturally (without induction) using salivette sampling devices (Sarstedt, Numberg, Germany) and were immediately stored frozen at –20 °C until assay. Samples were analysed with commercially available kits (Salimetrics, USA) at Macquarie University. Appropriate numbers of samples were thawed for determination of sAA activity, cortisol and progesterone according to the manufacturer's instructions. Thawed samples were centrifuged at 1500 × g for 15 min to collect clear saliva out of the cylindrical salivettes and this saliva was used without further processing for all assays. Wherever possible sAA and cortisol assays were performed consecutively without refreezing of the sample. All samples were brought to room temperature before adding to assay wells and all samples were analysed in duplicate. Thawed and centrifuged sAA saliva samples were diluted 1:200. The percentage of variability within and between the sAA assays was 4.4% and 9.3%, respectively. Thawed and centrifuged cortisol saliva samples were added in duplicate to appropriate wells followed by 200 μL of enzyme conjugate. The concentration of cortisol for each sample is determined by interpolation from a standard curve generated by plotting cortisol standards (0.012–3.0 μg/dL) against their average OD divided by the background OD (B/B_0). The percentage of variability within and between the cortisol assays was 3.5% and 5.05%, respectively.

2.5. Data analysis

The number of images correctly recalled was computed for each participant. Two independent raters scored a participant's description as correct if it could be clearly related to a particular image; the inter-rater reliability was very high ($\kappa = 0.83$). Demographic and psychometric data were analysed using 2 (sex: male/female) × 2 (condition: CPS/control) analyses of variance (ANOVAs). Salivary cortisol and alpha amylase data were analysed using 2 (sex: male/female) × 2 (condition: CPS/control) × 2 (time: baseline/post-stress) repeated measures ANOVAs. Memory recall data were analysed using 2 (sex: male/female) × 2 (condition:

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