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Acute stress impairs memory retrieval independent of time of day

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Summary It is widely recognized that acute stress and associated glucocorticoid stress responses yield memory-enhancing effects when the memory consolidation phase is targeted, while impairing effects are generally found with regard to memory retrieval performance. While some evidence exists that the memory-enhancing effects of consolidation stress are modulated by time of day, no study to date has investigated whether stress-induced retrieval deficits are also prone to such time of day effects. To address this issue, participants ($N = 76$) were exposed to a stressor or control condition before a retrieval test that probed for neutral and negative words learned 24 h before. Results show that stress exposure resulted in impaired retrieval of both neutral and negative words, but that time of day did not moderate this effect. This memory-impairing effect was larger for negative than for neutral information, and was significantly associated with stress-induced cortisol responses. The current findings demonstrate the robustness of stress-induced retrieval deficits throughout the day, in particular for emotional memory material, and further underscore the importance of cortisol reactivity in impairing memory retrieval.

1. Introduction

Stress activates the hypothalamic—pituitary—adrenal (HPA) axis, causing the release of glucocorticoids (GCs; corticosterone in rodents, cortisol (CORT) in humans) by the adrenal cortex. It is well established that in rodents as well as humans such GCs can influence memory processes by acting on brain structures central to memory (e.g., McGaugh and Roozendaal, 2002). Of critical importance is the observation that stress and heightened GC concentrations seem to enhance memory when released post-learning (i.e., during consolidation; e.g., Buchanan and Lovallo, 2001; Cahill et al., 2003; Smeets et al., 2008; however see Rimmele et al., 2003), but generally impair memory retrieval processes (e.g., de Quervain et al., 2000; Kuhlmann et al., 2005a,b; Smeets et al., 2006, 2008; Buchanan and Tranel, 2008). For example, in one of our previous studies (Smeets et al., 2008), we demonstrated that participants who were exposed to cold pressor stress after learning a list of neutral and emotional words performed better at a 24 h delayed recall test than participants in a no-stress control condition. Participants who received cold pressor stress before the memory retrieval phase, on the other hand, recalled fewer words than the no-stress controls. Moreover, both the memory-enhancing and memory-impairing effects were shown to be associated with stress-induced GC activity.

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Acute stress-induced GC memory effects are at least in part determined by the activation of intracellular mineralocorticoid (MR or type-I) and glucocorticoid (GR or type-II) receptors (e.g., de Kloet et al., 1999). The high affinity MRs are mainly occupied under normal, basal conditions while the low affinity GRs only become exceedingly saturated under conditions of raised CORT levels. When MRs are fully occupied and GRs are only partially activated, memory can be facilitated (Diamond et al., 1992; de Kloet et al., 1999). Alternatively, detrimental effects of high GC levels may occur when GRs become entirely saturated during stressful situations (e.g., Reul and de Kloet, 1985; Oitzl and de Kloet, 1992; de Kloet et al., 1999). This is important given that in humans, endogenous CORT levels follow a circadian rhythm, with higher levels in the morning phase (due to the CORT awakening response and the circadian rise of CORT; e.g., Fries et al., 2009) and continuously decreasing levels thereafter and in the afternoon. Thus, fluctuating CORT levels throughout the day — irrespective of potential stressors — already lead to a differential activation of MRs and GRs in the morning and afternoon and thus are capable of affecting memory (e.g., Rimmele et al., 2010). The modulation of memory performance by MRs and GRs will thus be a function of the presence or absence of exogenous (e.g., stress-induced) changes in circulating CORT levels and endogenous variations related to the circadian rhythm. In addition to the above-mentioned involvement of intracellular MRs and GRs in modulating memory performance, recent evidence also suggests rapid membrane bound effects of MRs (Joëls et al., 2008) and GRs (e.g., Roozendaal et al., 2010).

The importance of time of day in the relationship between stress, stress-induced CORT elevations, and memory performance so far has received only little attention in the literature. In fact, to the best of our knowledge, only one study (Maheu et al., 2005) has systematically investigated this issue. In that study, healthy young men were exposed to a psychosocial stressor before viewing emotional and neutral stimuli either in the morning hours or in the afternoon. Recall performance was tested one week later and compared to that of no-stress control groups. Maheu et al. (2005) found that stress exposure and the ensuing CORT increases impaired delayed recall of the emotional (but not neutral) stimuli in the morning stress group, while no such effect was apparent for the afternoon stress group. Moreover, a meta-analysis by Het et al. (2005) demonstrated that in the morning hours GC administration prior to learning impaired later memory performance while in the afternoon such GC administration on average resulted in slightly memory-enhancing effects. However, as properly noted by Het et al. (2005, pp. 779—780) "*This finding cannot be generalized to the category of studies which administered cortisol before retrieval [...] the negative effect of cortisol on retrieval might be relatively independent of the time of day.*" Indeed, whether heightened CORT levels differentially affect retrieval performance throughout the day remains open to empirical testing.

The current study therefore was set out to investigate the effect of stress and stress-induced CORT responses on memory retrieval performance in the morning versus afternoon hours. To this end, participants were required to encode neutral end emotional words and, 24 h later, were exposed to an acute stressor or no-stress control condition before delayed free recall was assessed. Crucially, half of them were tested for retrieval in the morning hours while the other half underwent the recall test in the afternoon. CORT was sampled via saliva throughout the retrieval session in order to investigate the contribution of stress-induced GC elevations on subsequent memory effects.

2. Materials and methods

2.1. Participants

Seventy-six healthy young undergraduates (42 women) with a mean age of 19.9 years (S.E. = 0.21; range: 18—25) participated in the current study. Study eligibility was assessed using a structured telephone interview, with cardiovascular diseases, severe physical illnesses (e.g., fibromyalgia), hypertension, endocrine disorders, current or lifetime psychopathology, substance abuse, heavy smoking (>10 cigarettes/day), or being on medication known to influence activity of the HPA axis serving as exclusion criteria. To ensure comparable CORT responses in men and women, women using oral contraceptives were also excluded from participation. In addition, women were mostly tested in the late luteal phase of their menstrual cycle when CORT responses of women appear to be similar to those of men (e.g., Kudielka and Kirschbaum, 2005). However, 11 of the 42 women were tested in the follicular instead of the late luteal phase due to continuing scheduling problems. Test protocols were approved by the standing Ethics Committee of the Faculty of Psychology and Neuroscience, Maastricht University. All participants signed a written informed consent and were financially compensated (10€) in return for their participation.

2.2. Stress induction

Stress was induced by exposing participants to the Socially Evaluated Cold Pressor Test (SECPT; Schwabe et al., 2008). In brief, participants were instructed to immerse their non-dominant hand up to and including the wrist in ice-cold (2 °C) water for as long as possible with a maximum of 3 min whilst being videotaped and watched by an unfamiliar experimenter. They were explicitly told that as the procedure could be very uncomfortable, they could remove their arm from the ice-cold water at their own discretion without consequences. Participants in the no-stress control condition underwent a similar procedure in that they submerged their non-dominant hand up to and including the wrist for 3 min in lukewarm (25 °C) water but were neither watched nor videotaped. Based on the previously reported mean hand immersion time for the SECPT (see Schwabe et al., 2008), we instructed participants in the no-stress control condition to remove their hand from the water after 2 or 3 min.

2.3. Declarative memory task

The current study used a word learning task that was previously used by Tollenaar et al. (2009) and that included 15 emotionally negative and 15 neutral words selected on Dutch arousal and valence ratings (Hermans and de Houwer, 1994) and matched for familiarity and word length. The 15 negative