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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.

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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 and 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

and 15 neutral words were presented on a 17 in. computer screen using PowerPoint (Microsoft Corporation) in capitals with font type Times New Roman, font size 80. Presentation duration of the words was 5 s, with a fixation cross being presented in between them for another 2 s. Presentation order of the words occurred pseudo-random so that no more than three words of the same valence were presented in succession. Words were presented on two successive learning trials, with participants being explicitly told that their memory for the words would be tested immediately following each trial by means of an immediate free recall task to ensure effortful encoding. However, we were mainly interested in participants' performance on a surprise delayed free recall task given to them 24 h later. Thus, we focused on the proportion of the 30 encoded words that were correctly recalled after 24 h. No mention of the upcoming delayed recall task was made at the memory encoding session.

2.4. Saliva sampling and biochemical analyses

Free CORT was measured in response to the SECPT as a measure of activity of the stress-responsive HPA axis. CORT data were obtained with synthetic Salivette (Sarstedt®, Etten-Leur, The Netherlands) devices and were stored at -20°C immediately on collection. Free CORT levels were determined by a commercially available luminescence immunoassay (IBL, Hamburg, Germany). Mean intra- and inter-assay coefficients of variation are typically less than 8% and 12%, respectively, and the lower and upper detection limits were $0.015\ \mu\text{g}/\text{dl}$ ($0.41\ \text{nmol}/\text{l}$) and $4.0\ \mu\text{g}/\text{dl}$ ($110.4\ \text{nmol}/\text{l}$), respectively.

2.5. Design and procedure

A 2(Group: stress vs. control) \times 2(Time of Day: morning vs. afternoon) between-subjects design was employed. Participants were pseudo-randomly assigned to the *morning stress* ($n = 26$; 14 women), the *afternoon stress* ($n = 26$; 14 women), the *morning control* ($n = 12$; 7 women), or the *afternoon control* ($n = 12$; 7 women) group such that men and women were distributed evenly across the experimental and the control groups. To allow for controlled saliva collection, participants were asked not to brush their teeth and were deprived of food, drinks, and heavy exercise at least 1 h prior

to the test sessions. None of the participants reported to have violated these requirements.

In the first individual test session that occurred between 11.30 and 13.30 h, all participants underwent the exact same procedure. During the first 10 min after arrival in the laboratory, participants were asked to relax and sit still in a comfortable chair during which time they were informed about the procedure and gave written informed consent. Subsequently, a first CORT sample was obtained and the memory encoding task was completed. After a second CORT sample was taken, participants were sent home overnight until the start of their second session.

The second individual test session took place either between 09 and 11 h (morning stress and morning control groups) or between 14 and 16 h (afternoon stress and afternoon control groups). Participants were first seated for a period of 10 min before baseline CORT was sampled (t_{+10}). Next, participants in the stress groups were exposed to the SECPT while controls underwent the warm water test (cf. supra). CORT was further sampled 10, 20, and 30 min after stress-onset (i.e., at t_{+20} , t_{+30} and t_{+40}). The delayed free recall task was administered 15–25 min after the beginning of stress exposure, when salivary CORT levels were expected to reach peak levels. After all measures were completed, participants were debriefed, paid, and thanked for their participation. Fig. 1 shows the timeline for both experimental sessions, with t_0 referring to the beginning of the test sessions.

2.6. Statistical analyses

Data was checked for non-normality using Q–Q plots and Shapiro–Wilk tests of normality, which showed skewness of the CORT data. Therefore, these data were log-transformed before use in subsequent analyses. CORT levels in Session 1 and CORT stress responses to the SECPT/control task in Session 2 were examined using repeated measures analyses of variance (ANOVAs) with Group and Time of Day as independent variables and CORT Sample as repeated measure. For each participant individually, we also computed a delta increase in CORT during Session 2 defined as maximum CORT concentration after the SECPT or control task minus baseline CORT concentration. Delta responses were analyzed using a univariate ANOVA. A repeated measures ANOVA with Group and Time of Day as independent variables and Valence as

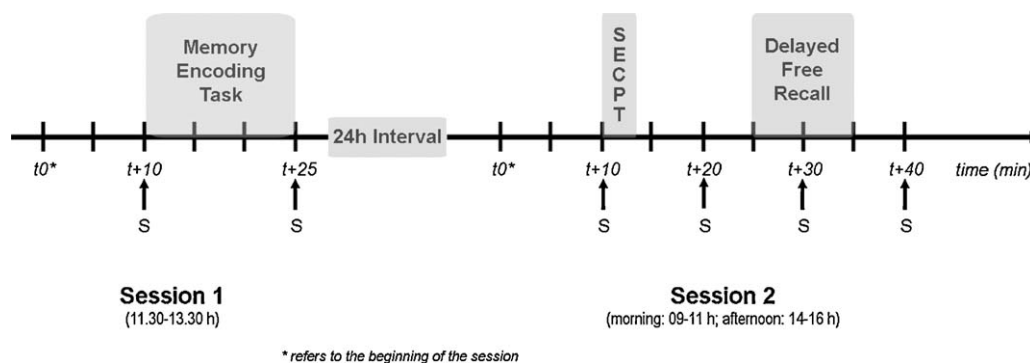


Figure 1 Timeline depicting the saliva sampling procedure (S = Salivette), the memory encoding task, stress induction (SECPT), and memory retrieval (delayed free recall test).

repeated measure was used to check whether groups differed with respect to their performance on the delayed free recall task. Finally, within the stress group Pearson correlations were computed between delayed free recall of neutral and negative words and delta CORT increases. When sphericity assumptions for the ANOVAs were violated, Greenhouse–Geisser corrected p -values are reported. Alpha was set at 0.05 and adjusted (Bonferroni) for multiple comparisons when necessary. In case of (borderline) significant results, ANOVAs are supplemented with partial eta squared (η_p^2) values as a measure of effect size.

3. Results¹

3.1. CORT concentrations at memory encoding

Fig. 2 shows CORT concentrations at memory encoding (Session 1) for the morning stress, morning control, afternoon stress, and afternoon control groups. ANOVA showed a significant main effect of CORT Sample [$F(1,72) = 14.04$; $p < 0.001$; $\eta_p^2 = 0.16$], but no main effects of Group, Time of Day, or any interactive effects. The main effect of CORT Sample was qualified by slight decreases in CORT concentrations from the beginning to the end of Session 1.

3.2. CORT responses to the SECPT

Mean hand immersion time did not differ between the various groups (means \pm S.E. being $167\text{ s} \pm 4.57$ for the morning stress, $165\text{ s} \pm 4.52$ for the morning control, $169\text{ s} \pm 4.37$ for the afternoon stress, and $165\text{ s} \pm 4.52$ for the afternoon control groups; [all $F_s < 1$; all $p_s > 0.59$]). Fig. 2 shows CORT responses to the SECPT/control task at Session 2. ANOVA showed significant interactive effects of Group \times CORT Sample [$F(3,216) = 94.41$; $p < 0.001$; $\eta_p^2 = 0.57$] and Time of Day \times CORT Sample [$F(3,216) = 9.40$; $p < 0.001$; $\eta_p^2 = 0.12$]. Therefore, repeated measures ANOVAs were run for the morning and afternoon groups separately.

For the morning groups, ANOVA yielded significant main effects of Group [$F(1,36) = 11.71$; $p = 0.002$; $\eta_p^2 = 0.25$] and CORT Sample [$F(3,108) = 6.23$; $p = 0.002$; $\eta_p^2 = 0.15$] and a significant Group \times CORT Sample interaction [$F(3,108) = 44.09$; $p < 0.001$; $\eta_p^2 = 0.55$]. Follow-up tests showed that the morning stress group displayed an increase in CORT from

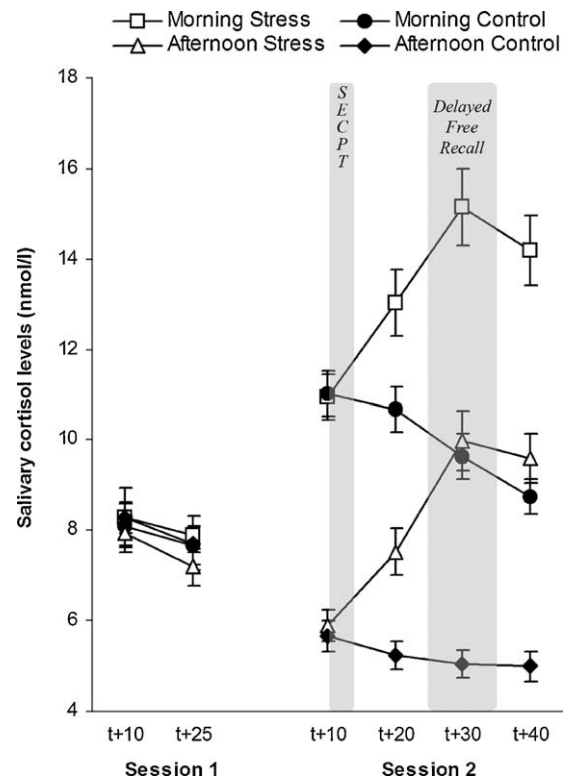


Figure 2 Cortisol levels throughout Session 1 (memory encoding task) and Session 2 (stress induction and memory retrieval task). Error bars represent standard error of mean (S.E.).

baseline to after the start of the SECPT (i.e., t_{+20} ; $p < 0.001$), further increased from t_{+20} to t_{+30} ($p < 0.001$), and decreased from t_{+30} to t_{+40} ($p = 0.049$). The morning control group on the other hand showed a non-significant change from baseline to t_{+20} ($p = 0.32$) and then decreased from t_{+20} to t_{+30} ($p = 0.015$) and t_{+30} to t_{+40} ($p = 0.004$).

Similarly, with regard to the afternoon groups ANOVA yielded significant main effects of Group [$F(1,36) = 16.98$; $p < 0.001$; $\eta_p^2 = 0.32$] and CORT Sample [$F(3,108) = 20.42$; $p < 0.001$; $\eta_p^2 = 0.36$] and a significant Group \times CORT Sample interaction [$F(3,108) = 51.03$; $p < 0.001$; $\eta_p^2 = 0.59$]. Follow-up tests showed that the afternoon stress group displayed an increase in CORT from baseline to t_{+20} ($p < 0.001$) and from t_{+20} to t_{+30} ($p < 0.001$), but remained stable between t_{+30} and t_{+40} ($p > 0.99$). CORT concentrations in the afternoon control group did not show changes over time (baseline to t_{+20} : $p = 0.75$; t_{+20} to t_{+30} : $p = 0.94$; t_{+30} to t_{+40} : $p > 0.99$).

As is apparent from inspecting Fig. 2, the CORT response pattern to the SECPT did not differ between the morning and afternoon group. This was confirmed by an ANOVA on the delta CORT responses showing significant differences for Group [$F(1,72) = 74.43$; $p < 0.001$; $\eta_p^2 = 0.51$] but not Time of Day [$F(1,72) < 1$; $p > 0.99$] or a Group \times Time of Day interaction [$F(1,72) < 1$; $p > 0.92$], with the stress group showing increases in CORT in response to the SECPT (mean $_{\text{delta CORT}} = 4.43$; S.E. = 0.36; $p < 0.001$) while overall the control group slightly decreased in CORT concentrations throughout Session 2 (mean $_{\text{delta CORT}} = -0.27$; S.E. = 0.14; $p = 0.056$).

¹ As CORT responses may differ between men and women (e.g., Kudielka and Kirschbaum, 2005), we repeated the ANOVAs pertaining to the CORT responses with Sex included as an independent variable. No main or interactive effects involving Sex were detected. Moreover, specific sex differences have also been reported in the relationship between CORT stress responses and declarative memory performance (e.g., Wolf et al., 2001). In the present study, however, no main or interactive effects involving Sex were found for the memory data. Similar analyses with respect to differences in menstrual cycle phase between the various groups (*morning stress group*: 12 women in the late luteal phase, 2 women in the follicular phase, and 12 men; *morning control group*: 3 women in the late luteal phase, 4 women in the follicular phase, and 5 men; *afternoon stress group*: 12 women in the late luteal phase, 2 women in the follicular phase, and 12 men; *afternoon control group*: 4 women in the late luteal phase, 3 women in the follicular phase, and 5 men) were shown not to have influenced the current results.

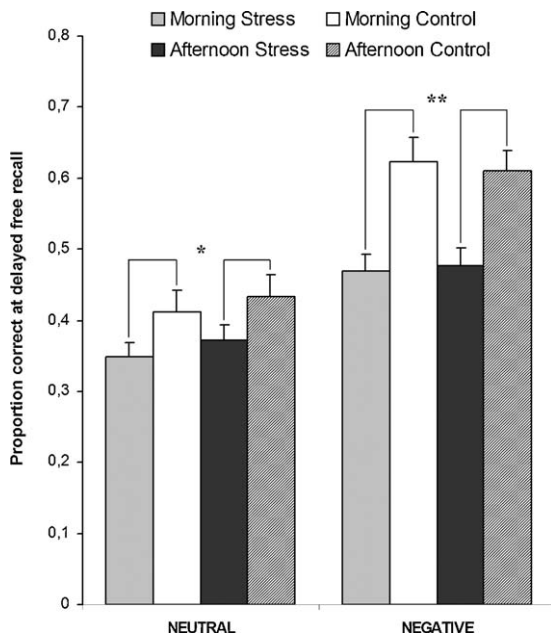


Figure 3 Proportion correct recall of neutral and negative words at delayed free recall. Error bars represent standard error of mean (S.E.). * $p < 0.05$. ** $p < 0.001$.

3.3. Declarative memory task

Mean proportion correct delayed recall of neutral and negative words is shown in Fig. 3. ANOVA showed main effects of Group [$F(1,72) = 27.39$; $p < 0.001$; $\eta_p^2 = 0.28$] and Valence [$F(1,72) = 64.35$; $p < 0.001$; $\eta_p^2 = 0.47$], as well as a significant Group \times Valence interaction [$F(1,72) = 4.91$; $p < 0.030$; $\eta_p^2 = 0.06$]. Further exploring this interaction, univariate ANOVAs with Group and Time of Day as independent variables were run for delayed recall of neutral and negative words separately. For delayed recall of neutral words, ANOVA yielded a significant effect of Group [$F(1,72) = 6.01$; $p = 0.017$; $\eta_p^2 = 0.08$], but no main effect of Time of Day [$F(1,72) = 0.92$; $p = 0.34$] or a Group \times Time of Day interaction [$F(1,72) = 0.01$; $p = 0.91$]. Overall, the control group outperformed the stress group with regard to proportion correct recall of neutral words. For delayed recall of negative words, similar results were found in that a significant effect of Group [$F(1,72) = 25.76$; $p < 0.001$; $\eta_p^2 = 0.26$] appeared, but no main effect of Time of Day [$F(1,72) = 0.01$; $p = 0.91$] or a Group \times Time of Day interaction [$F(1,72) = 0.25$; $p = 0.62$]. Specifically, participants who were exposed to the SECPT recalled fewer negative words than the control group at delayed free recall.² Finally, specific contrast analyses confirmed that the memory-impairing effect of retrieval stress

² Similar analyses did not reveal significant main or interactive effects involving Group or Time of Day for the memory-encoding task (i.e., learning trials 1 and 2 at Session 1). Moreover, when delayed recall was adjusted for recall performance following the final learning trial, equivalent main and interactive effects regarding delayed free recall performance were found as those described above. Thus, it is safe to assume that the non-significant findings regarding Time of Day were unaffected by encoding performance 24 h earlier.

for negative words was larger than that for neutral words ($p < 0.001$).

Pearson's correlations between delta CORT responses and delayed free recall of neutral and negative words showed that within the SECPT group as a whole, CORT responses were significantly associated with proportion correct recall of negative words ($r = -.34$; $p = 0.01$) and marginally significant with proportion correct recall of neutral words ($r = -.27$; $p = 0.06$). Separate for time of day, the correlations between CORT responses and correct recall of negative and neutral words in the morning stress group were $-.33$ and $-.36$, respectively. For the afternoon stress group, these correlations were $-.37$ and $-.16$, respectively.

4. Discussion

The current study has two main findings. First, compared to the no-stress control groups, exposure to the SECPT before retrieval testing impaired recall performance in the morning as well as the afternoon. This was true for both neutral and emotional stimuli, although impaired retrieval performance following stress was of greater magnitude for the emotional stimuli (for comparable findings, see e.g., Kuhlmann et al., 2005a,b; Buchanan et al., 2006; Smeets et al., 2008). Second, the current results confirm previous work showing that stress-induced CORT reactivity is associated with memory-impairing effects at retrieval. Specifically, within the stress group CORT responses to the SECPT were negatively correlated with delayed recall performance.

The fact that stress-induced retrieval deficits appear to be irrespective of time of day fits well with studies that have independently demonstrated stress and/or GC-induced retrieval impairments in the morning (e.g., Wolf et al., 1998, 2001; Tops et al., 2003; Kuhlmann et al., 2005b) and afternoon (e.g., Lupien et al., 2002; Kuhlmann et al., 2005a; Buchanan et al., 2006; Smeets et al., 2006, 2008; Buchanan and Tranel, 2008). To some extent, the current findings are at variance with previous observations showing that time of day might be an important modulator of the relationship between stress and memory (Lupien et al., 1999, 2002; Maheu et al., 2005). In a first study by Lupien et al. (1999), healthy young individuals received GCs intravenously in the morning hours prior to memory encoding, and detrimental effects on recall performance were found. In a later study (Lupien et al., 2002) in which participants were given a similar dose of GCs prior to memory encoding but this time in the late afternoon, recall performance remained unchanged compared to a placebo condition. In a more systematic investigation of time of day effects (Maheu et al., 2005), participants encoded emotional and neutral stimuli after having undergone a psychosocial stressor either in the morning hours or in the afternoon. Maheu et al. found that those participants who in the morning hours were stressed during encoding displayed impaired delayed recall of the emotional stimuli compared to a no-stress control group, while no such effect was found for the afternoon encoding stress group. The present study, in contrast to those of Lupien et al. (1999, 2002) and Maheu et al. (2005), dealt with time of day and stress-induced retrieval deficits. Here, we provide experimental evidence for the idea that the negative effect of stress and the ensuing CORT responses on memory retrieval might be relatively independent of time of day (cf. Het et al., 2005). These

apparently discrepant findings regarding time of day could imply a distinct involvement of GRs in the consolidation enhancing effect of stress-induced CORT responses versus their impairing effect on retrieval performance. In particular, it may be the case that stress-induced GC effects on retrieval processes reflect rapid membrane bound non-genomic effects, while the enhancing effects on memory consolidation might rely more strongly on intracellular genomic GR effects that might be more strongly influenced by time of day (e.g., Nader et al., 2010; but see Roozendaal et al., 2010 for evidence of membrane bound GR involvement in enhancing memory consolidation).

The idea of variation in receptor sensitivity over the course of the day (Nader et al., 2010) could also explain why in the current study stress-induced CORT levels in the morning and afternoon were found to have similar effects on retrieval performance despite their large differences in absolute concentrations. Clearly, a mere shift in the MR/GR balance (e.g., Oitzl et al., 2010) cannot explain this finding as it was also demonstrated that the morning control group reached CORT levels during retrieval testing comparable with those of the afternoon stress group yet only this latter group displayed retrieval deficits. Evidently, this implies that absolute CORT concentrations are not crucially concerned with deteriorated retrieval performance. Rather, it seems likely that the rapid rise in CORT levels and/or increased sympathetic activity, possibly together with alterations in receptor sensitivity, is involved in stress-induced retrieval deficits.

It should be noted that Schoofs and Wolf (2009) recently were unable to find evidence of impaired retrieval performance following stress exposure in a sample of naturally cycling (i.e., not on oral contraceptives) young women who were tested in their luteal phase. Schoofs and Wolf argued that elevated gonadal steroids, which are characteristic of the luteal phase and are related to a reduced GC sensitivity, might have resulted in a missing impact of stress on retrieval performance. Here, however, we demonstrate robust stress-induced retrieval deficits within a sample of healthy young undergraduates of whom the majority were naturally cycling women tested in the luteal phase. The present findings are reminiscent of those of Kuhlmann et al. (2005a), who reported that exogenous CORT elevations impaired memory retrieval in naturally cycling women but not in women using oral contraceptives. Whatever the case may be, these inconsistent findings highlight a need for further investigating the precise role of menstrual cycle associated changes in sex steroid (e.g., estradiol, progesterone) concentrations in the modulation of memory performance by stress and GCs. Also note that in the present study CORT responses to the SECPT did not differ between the morning and afternoon group, a finding that accords well with previous observations of Kudielka et al. (2004). Collectively, this suggests that the impact of time of day on stress-induced salivary CORT elevations appears to be rather small (however, see Dickerson and Kemeny, 2004, for a meta-analysis showing that CORT responses on average are descriptively smaller in the morning hours compared to the afternoon).

A limitation of the present study is that it did not assess any markers of adrenergic activity (e.g., via salivary alpha-amylase). This is germane given that in order for stress-induced retrieval deficits to occur, both rises in GC levels

and concurrent noradrenergic activation in the basolateral part of the amygdala (BLA) are required (e.g., Roozendaal et al., 2006, 2008; de Quervain et al., 2007). de Quervain et al. (2007), for example, demonstrated that the detrimental effects of GC administration on the retrieval of emotionally arousing words could be blocked by administration of the central β -blocker propranolol. Thus, we can only speculate that in the current study, where retrieval testing took place at a time following stress exposure when salivary CORT levels were expected to reach peak levels and stress-induced retrieval deficits were consistently observed across both stress groups, noradrenergic activity in the BLA may nonetheless have been elevated by the arousing nature of the testing situation (cf. Kuhlmann and Wolf, 2006).

All in all, the current results suggest that stress-induced retrieval deficits occur reliably and seemingly independent of time of day, that these retrieval deficits apparently do not rely on absolute CORT concentrations, and once more demonstrate the importance of stress-induced CORT reactivity in modulating memory performance.

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Conflict of interest

No conflicts of interest are declared.

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