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Context-dependent enhancement of declarative memory performance following acute psychosocial stress

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Abstract

Studies on how acute stress affects learning and memory have yielded inconsistent findings, with some studies reporting enhancing effects while others report impairing effects. Recently, Joëls et al. [Joëls, M., Pu, Z., Wiegert, O., Oitzl, M.S., Krugers, H.J., 2006. Learning under stress: how does it work? Trends in Cognitive Sciences, 10, 152–158] argued that stress will enhance memory only when the memory acquisition phase and stressor share the same spatiotemporal context (i.e., context-congruency). The current study tested this hypothesis by looking at whether context-congruent stress enhances declarative memory performance. Undergraduates were assigned to a *personality stress* group ($n = 16$), a *memory stress* group ($n = 18$), or a *no-stress control* group ($n = 18$). While being exposed to the acute stressor or a control task, participants encoded personality- and memory-related words and were tested for free recall 24 h later. Relative to controls, stress significantly enhanced recall of context-congruent words, but only for personality words. This suggests that acute stress may strengthen the consolidation of memory material when the stressor matches the to-be-remembered information in place and time.

Keywords: Acute stress; Glucocorticoids (GCs); Trier Social Stress Test (TSST); Context; Declarative memory

Most people are familiar with highly stressful events. Exposure to such events is known to trigger a variety of physiological reactions, of which many are related to the activation of stress-responsive sympathoadrenal medullary (SAM) and hypothalamic–pituitary–adrenal (HPA) axes. A plethora of research has revealed that secretion of glucocorticoids (GCs) due to HPA axis stimulation may modulate memory functioning (e.g., de Kloet et al., 1999; McGaugh, 2000; Roozendaal, 2000). However, the precise direction of stress-induced GC effects on memory performance is far from clear. Animal studies, for example, have shown that GCs can have facilitating (e.g., on aversive conditioning), but also impairing effects on memory (e.g., de Kloet et al., 1999; Lupien and McEwen, 1997; McGaugh and Roozendaal, 2002). Similarly, studies relying on human participants have reported that acute GC administration may enhance or disrupt memory, yet the precise conditions under which these effects occur are ill-understood (for reviews, see Het et al., 2005; Lupien et al., 2005; Lupien and Lepage, 2001; Wolf, 2003).

One critical variable identified so far is the timing of GC administration or stress exposure. When participants are exposed to acute stress or given GCs prior to the memory retrieval phase, a significant decrease in memory performance is noted (de Quervain et al., 2000; Wolf et al., 2004). Moreover, the effects of GC administration or stress exposure on memory performance also depend on the valence of the material being studied (e.g., Jelicic et al., 2004; Kuhlmann et al., 2005a,b; Smeets et al., 2006; Tops et al., 2003). That is, when applied prior to encoding and recall is tested immediately afterwards, acute stress or GC administration generally impairs memory for neutral stimuli while memory for emotionally positive and negative stimuli appears to be relatively immune to these detrimental effects. On the other hand, when stress or GC administration is employed after consolidation has taken place and delayed recall tests are used, emotional stimuli tend to be impaired more so than neutral ones. On a related note, emotional arousal elicited by the memory material is also important (e.g., Abercrombie et al., 2006; Kuhlmann and Wolf, 2006). It seems that when the to-be-remembered stimuli elicit high levels of emotional arousal, SAM driven stress responses

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in conjunction with GC stress responses may result in memory facilitation for these stimuli in comparison to memory for neutral, low arousing material.

Although a number of variables that modulate the effects of acute stress on memory performance have been identified, the precise nature of the effects remains unclear and a comprehensive framework that may account for the contradictory findings is lacking. Recently, Joëls et al. (2006) have made a first attempt to formulate such an accommodating framework. These authors propose that stress will only enhance memory performance when two conditions are met: first, exposure to stress must be experienced in the context and around the time of learning and, secondly, the brain regions targeted by GCs released during stress exposure should be the same as those activated by the memory task. Thus, stress will promote learning only when its spatiotemporal context is congruent to the memory material, such as is the case when an individual is stressed due to an upcoming exam and learns the subject matter while being stressed. In addition, the memory enhancing effect will only be apparent when stress impacts on the same brain regions as the task at hand, such as when the psychological stress associated with exams impacts upon the hippocampus and the recall task (i.e., exam) also probes for knowledge that is mainly hippocampal-dependent (e.g., factual knowledge, but not procedural memory).

The present study was specifically designed to test the framework of Joëls et al. (2006). In short, our aim was to determine whether exposure to a psychosocial stressor may indeed prove beneficial to performance on declarative memory tasks that are context-related to the applied stressor. To this end, concurrent with learning a list of words that were personality- and memory-related, participants were exposed to a stress task that was focused either on a personality theme or a memory theme. Twenty-four hours later, delayed recall was assessed and compared to a no-stress control condition. Based on Joëls et al. (2006), we hypothesized that relative to non-stressed controls, participants exposed to the acute stressor would show enhanced delayed recall of words that were in congruence with the theme of the stressor.

1. Methods

1.1. Participants

Our sample consisted of 52 young healthy undergraduate students (13 men, 39 women) with a normal body mass index (BMI). Their mean age was 23.08 years (S.D. = 3.81). Participants were excluded from the study when they suffered from endocrine disorders, cardiovascular diseases, other severe medical illnesses (e.g., fibromyalgia), or were on medications known to affect HPA-axis functioning (except oral contraceptives; see below). Test protocols were approved by the standing ethics committee of the Psychology Faculty of Maastricht University. All participants signed a written informed consent and were given course credit in return for their participation.

1.2. Materials

1.2.1. Profile of Mood States

Subjective stress was measured with the Profile of Mood States (POMS; McNair et al., 1992). The POMS is a widely used self-report measure of typical and persistent mood reactions to current life situations. Participants indicate to what extent they agree with adjectives describing their current mood or feelings on five-point scales (anchors: 0 = *not at all*; 4 = *extremely*). The 32-item POMS consists of five subscales (i.e., depression–dejection, anger–hostility, fatigue–inertia, vigor–activity, and tension–anxiety) from which a total negative mood score can be calculated, with higher POMS scores reflecting very negative mood. The POMS has excellent psychometric properties (Lezak, 2004; McNair et al., 1992). We used two Dutch parallel versions of the POMS which have been proven to be valid and reliable (de Groot, 1991; Wald and Mellenbergh, 1990). These two versions were counterbalanced within and across groups.

1.2.2. Trier Social Stress Test (TSST)

The Trier Social Stress Test (TSST; Kirschbaum et al., 1993) is a valid and reliable procedure to induce cortisol stress responses (e.g., Dickerson and Kemeny, 2004; Kirschbaum et al., 1992). We employed a modified version of the TSST basically consisting of a 5 min preparation period, a 5 min mental arithmetic task, and a 6 min free speech in front of an audience while being videotaped. The TSST was modified in such a way that the topic of the free speech was either personality- or memory-related (see Section 1.3 for more details).

1.2.3. Verbal declarative memory task

Participants were required to listen to 2 word lists of 12 words each, with one list consisting of memory words (e.g., ''knowledge'', ''intellect'') and the other containing personality words (e.g., ''anxious'', ''modest''). Words were chosen from the Affective Norms for English Words (ANEW; Bradley and Lang, 1999) and were unanimously categorized as personality or memory words, respectively, in a pilot study ($N = 10$ undergraduate students). Data drawn from the ANEW normative ratings showed that memory and personality words did not differ with respect to mean valence, arousal, dominance, or word frequency (all $ts < 1$; all $ps > .43$). Word lists were audio taped and played back on a digital voice recorder, thus ensuring that all participants heard the words at the same pace, tone of voice, volume, and intonation. Presentation order of the word lists was counterbalanced within and across groups, and lists were presented on two successive learning trials. Participants were explicitly told that their memory for the words would be tested immediately following presentation of the word lists by means of an immediate free recall task. However, we were primarily interested in a surprise delayed free recall test given to them 24 h later.[1]

1.2.4. Heart rate measurement

Heart rate was monitored continuously using portable transmission devices (Polar® Sport Profi S810i). Heart beats per minute (bpm) were averaged over 5 min intervals beginning with the 5 min before stress exposure or filler task and ending after a 30 min total measurement interval had been completed.

1.2.5. Saliva sampling and biochemical analyses

Cortisol data were obtained with cotton Salivette (Sarstedt®, Etten-Leur, The Netherlands) devices. Saliva samples were not centrifuged and were immediately stored at −40 °C on collection. Salivary free cortisol levels were determined in duplicate by direct radioimmunoassay (University of Liège, Belgium), including a competition reaction between ^{125}iodohistamine-cortisol and anticortisol serum made against the 3-carboxymethyloxime–bovine serum albumin conjugate. After overnight incubation at 4 °C of 50 μl saliva, separation of free and antibody-bound ^{125}iodohistamine-cortisol was performed via a conventional second-antibody method. In order to reduce sources of variability, both samples from each participant were analyzed in the same assay. Mean intra- and inter-assay coefficients of variation were less than 5% and 9%, respectively.

[1] In the current study, we were primarily interested in whether congruency between stressor and the to-be-encoded memory material affects subsequent memory performance. In order to eliminate the effects of acute stress and GC elevations on retrieval processes (e.g., de Quervain et al., 2000), the delayed recall test was administered 24 h after initial learning took place.

1.3. Design and procedure

All participants were tested individually in experimental sessions run between 08.30 a.m. and 12.00 a.m. The entire test session never exceeded 45 min. To allow for objective controlled cortisol sampling, all participants refrained from food, drinks, smoking, and heavy exercise at least 1 h prior to the test phase. None of the participants reported to have violated these requirements. Participants were randomly assigned to one of two stress groups, or a no-stress control group. In the first group ($n = 16$), participants were exposed to a modified version of the TSST in which they had to perform a 5 min mental arithmetic task and engage in a 6 min free speech about their personality while standing in front of a live audience and being videotaped (i.e., the *personality stress* group). Similarly, participants in the *memory stress* group ($n = 18$) had to perform the modified TSST, but were asked to give a speech concerning the quality of their memory. To increase the stressful nature of the TSSTs, both groups had to deliver the speech in English (i.e., a non-native language). Participants in the no-stress *control* group ($n = 18$) were shown an emotionally neutral video fragment of an animation film (i.e., filler task). TSSTs and filler task were equal in duration. The extent to which they elicited stress was determined both subjectively (i.e., participants completed the POMS before and after the TSST or filler task) and objectively (i.e., by continuously measuring heart rate and collecting cortisol data). Groups did not differ with respect to mean age [$F(2, 49) = 1.42$; $p = .25$; $\eta_p^2 = .06$], proportion men versus women [$\chi^2(3, N = 52) = 0.48$; $p = .85$; Cramer's $V = .10$], or smoker/non-smoker ratio [$\chi^2(3, N = 52) = 0.08$; $p = .99$; Cramer's $V = .05$] (see Table 1 for means).

Upon arrival in the laboratory, participants signed a consent form and were familiarized with the heart rate measurement device, which then was connected and activated. During the first 5 min (T01-05), participants were asked to fill out the POMS and a first cortisol measure was collected. Next, personality and memory stress groups were exposed to the adapted version of the TSST and the no-stress controls were given a filler task. Integrated at the end of the TSST or filler task, participants were presented with the verbal declarative memory task with the explicit instruction that their memory would be tested afterwards (T06-25). Following presentation, an immediate free recall task was administered and participants were instructed to fill out the POMS a second time. At the end of the session, a second cortisol sample was collected and the heart rate measurement was ended (T26-30). Finally, participants were asked to return 24 h later to complete the key measure of interest, i.e., the surprise 24 h delayed recall test. To reduce the likelihood that participants would rehearse the word lists, they were told that their heart rate data and immediate recall test would be analyzed, and that their performance would be discussed with them the next day. No mention of an upcoming memory test was made. When they returned 24 h later, a delayed free recall test for words from both lists was administered. None of the participants indicated that they had expected a delayed recall test.

1.4. Statistical analyses

As a measure of subjective feelings of distress and negative affect following the TSST or filler task, mean increases in POMS scores were calculated as [POMS score at T30 − POMS score at T05] and subjected to a one-way (group: personality stress versus memory stress versus control) analysis of variance (ANOVA). Heart beats were averaged over 5 min intervals for between-group analysis. Due to technical failures, heart rate data from five individuals were lost. Mean bpm was analyzed using a 3 (group: personality stress versus memory stress versus control) × 6 (time: T01–05 versus T06–10 versus T11–15 versus T16–20 versus T21–25 versus T26–30) ANOVA with time as repeated factor. Similarly, cortisol responses were analyzed using a 3 (group: personality stress versus memory stress versus control) × 2 (time: T05 versus T30) ANOVA with time as repeated factor. To check whether stress affected initial learning as assessed by the immediate free recall test, a 3 (group: personality stress vesus memory stress versus control) × 2 (word type: personality words versus memory words) ANOVA with word type as repeated factor was conducted. Delayed free recall performance was analyzed using a 3 (group: personality stress versus memory stress versus control) × 2 (word type: personality words versus memory words) ANOVA with word type as repeated factor. Similarly, an ANOVA controlling for potential between-group variance in initially encoded words (i.e., by expressing delayed free recall performance as the percentage of words remembered in relation to immediate free recall performance; see Kuhlmann et al., 2005a,b) was conducted. Within the stress groups, Spearman's rho correlations (two-tailed) between the memory parameters and cortisol and heart rate responses were calculated. Where appropriate, partial eta squared (η_p^2) was calculated as a measure of effect size. When sphericity assumptions were violated, Greenhouse–Geisser corrected p-values were determined. Alpha was set at .05 unless specified otherwise, and adjusted (Bonferroni) for multiple comparisons where necessary.

Table 1
Means (±S.E.M.) for background characteristics of participants in the memory stress, personality stress, and no-stress control group

	Memory stress group ($n = 18$)	Personality stress group ($n = 16$)	Control group ($n = 18$)
Age (years)	21.9 ± 0.46	23.9 ± 1.17	23.5 ± 0.99
Male/female ratio	4/14	5/11	4/14
Proportion OC users[a]	64%	73%	71%
Smoker/non-smoker ratio	4/14	3/13	4/14

[a] OC: oral contraceptives; proportion OC users reflects number of women using OCs divided by total number of women.

2. Results

2.1. Group comparisons with respect to self-reported menstrual cycle phase and oral contraceptive use

Based on days since last menstrual period onset, female participants self-reported the phase of menstrual cycle (i.e., follicular, midcycle, or luteal), as well as their use of oral contraceptives. Nineteen of them reported being in the follicular, 11 in the midcycle, and 4 in the luteal phase of their menstrual cycle. Twenty-four women indicated that they actively used oral contraceptives. Pearson chi-square exact tests were used to evaluate group differences in menstrual cycle phase and oral contraceptive use, but no significant differences emerged (all $ps > .37$).

2.2. Subjective feelings of distress (POMS)

Participants indicated being subjectively stressed in both the personality stress and the memory stress group, as indexed by mean increases in POMS scores (personality stress group $M = 8.69$, S.D. = 3.03; memory stress group $M = 5.17$, S.D. = 2.50), while a decrease was noted for the control group ($M = -1.94$, S.D. = 2.58); [$F(2, 49) = 4.02$; $p < .03$; $\eta_p^2 = .14$].

2.3. Heart rate data

Fig. 1 shows bpm for stress groups and the control group. ANOVA yielded significant main effects of group [$F(2, 44) = 8.33$; $p = .001$; $\eta_p^2 = .28$] and time [$F(5, 220) = 31.45$; $p < .001$; $\eta_p^2 = .42$], as well as a critical group × time interaction [$F(10, 220) = 16.35$; $p < .001$; $\eta_p^2 = .43$]. Follow-up tests confirmed that relative to the filler task in the control group, participants in both stress groups displayed significant increases in mean bpm after TSST onset (all $ts > 5.28$; all $ps < .001$).

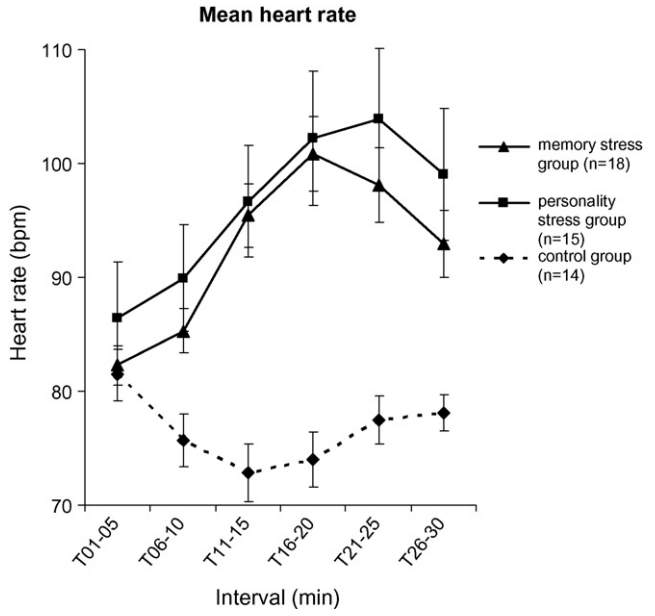

Fig. 1. Mean heart rate expressed in beats per minute (bpm) for the memory stress, personality stress, and no-stress control groups over time. Participants received a stress or filler task in the T06-25 minute interval. Error bars represent the standard error of mean (S.E.).

2.4. Cortisol stress responses

Cortisol data were examined for outliers, but none were identified. Fig. 2 shows increases in cortisol levels for the personality stress, memory stress, and the control group. As expected, a significant main effect of time [$F(1, 49) = 21.77$; $p < .001$; $\eta_p^2 = .31$] and a significant group × time interaction [$F(2, 49) = 7.48$; $p = .001$; $\eta_p^2 = 0.23$] were found in the absence of a main effect of group [$F(2, 49) = 1.61$; $p = .21$; $\eta_p^2 = 0.06$]. Follow-up t-tests showed that compared to the control group, the personality stress and memory stress groups displayed significant increases in cortisol (both ts > 3.17; both ps $< .01$).[2] Previous research has indicated that cortisol increases larger than 2.5 nmol/l reflect cortisol secretory episodes (Van Cauter and Refetoff, 1985) and can be considered a clear-cut cortisol response (see, e.g., Kirschbaum et al., 1993; Schommer et al., 2003). Mean delta cortisol increases in the current study were 3.97 nmol/l (S.D. = 3.74) for the personality stress, 3.53 nmol/l (S.D. = 4.73) for the memory stress, and −0.38 nmol/l (S.D. = 2.02) for the control group.

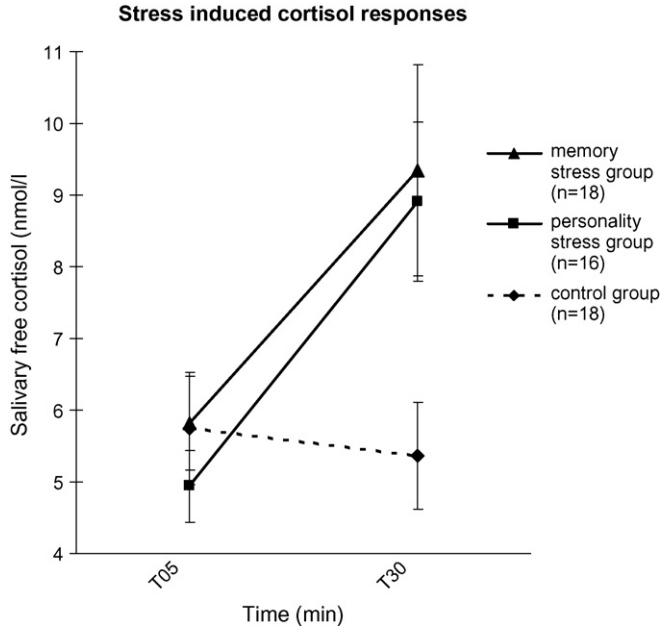

Fig. 2. Mean salivary free cortisol levels (nmol/l) for memory stress, personality stress, and no-stress control groups. Error bars represent the standard error of mean (S.E.).

To check whether the use of oral contraceptives influenced cortisol responses (e.g., Kirschbaum et al., 1999), cortisol data from the personality stress and memory stress group were collapsed and subjected to an independent samples t-test. Although women who used oral contraceptives showed cortisol responses that were much smaller than naturally cycling women, this difference fell short of significance (with means of $M = 2.32$, S.D. = 3.36 and $M = 4.52$, S.D. = 3.62 for women using oral contraceptives and naturally cycling women, respectively [$t(23) = 1.44$; $p = .16$]).

2.5. Immediate free recall performance

Mean proportion correctly recalled personality words on the immediate free recall test were .48, .47, and .48 for the memory stress, the personality stress, and control group, respectively. For memory words, means were .44, .41, and .50 for the memory stress, the personality stress, and control group, respectively. ANOVA showed that the groups did not differ with respect to their performance on the immediate free recall test, as evidenced by the absence of significant main effects of group and word type, and a non-significant group × word type interaction (all Fs < 1.37; all ps $> .26$).

2.6. Delayed free recall performance

Fig. 3 shows delayed free recall performance of the three groups. Repeated measures ANOVA yielded a significant critical group × word type interaction [$F(2, 49) = 4.10$; $p = .02$; $\eta_p^2 = .14$] in the absence of significant main effects of group [$F(2, 49) = 0.35$; $p < .70$; $\eta_p^2 = .01$] or word type [$F(1, 49) = 2.81$; $p = .10$; $\eta_p^2 = .05$]. Follow-up t-tests indicated that relative to the memory stress and the control group, the personality stress group showed enhanced delayed recall of personality words (both ps $< .03$), but that memory words were not affected. Within the personality stress group, cortisol ($r = .58$; $p < .05$) but not heart rate responses ($r = -.04$) were significantly related to correct recall of personality words. No significant correlations emerged between cortisol and heart rate responses and recall of memory words within the personality

[2] Note that as sessions were run between 08.30 a.m. and 12.00 a.m., one could argue that diurnal fluctuations in free cortisol might have affected cortisol responses. However, in line with Kudielka et al. (2004), cortisol responses in the present study were not affected by time of day.

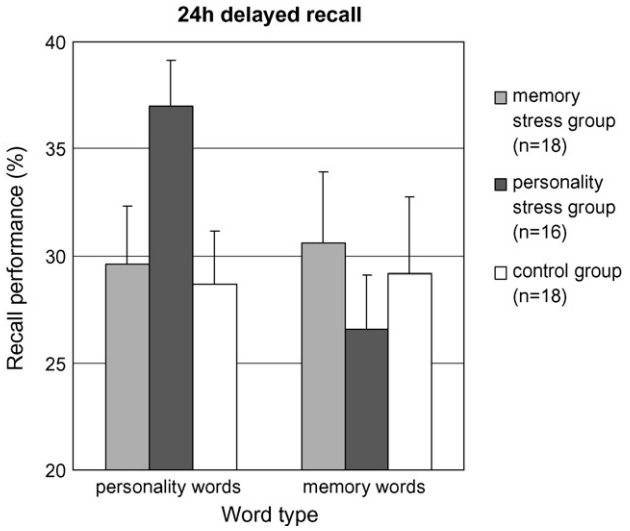

Fig. 3. Mean scores on the delayed free recall test for the three groups. Error bars represent the standard error of mean (S.E.).

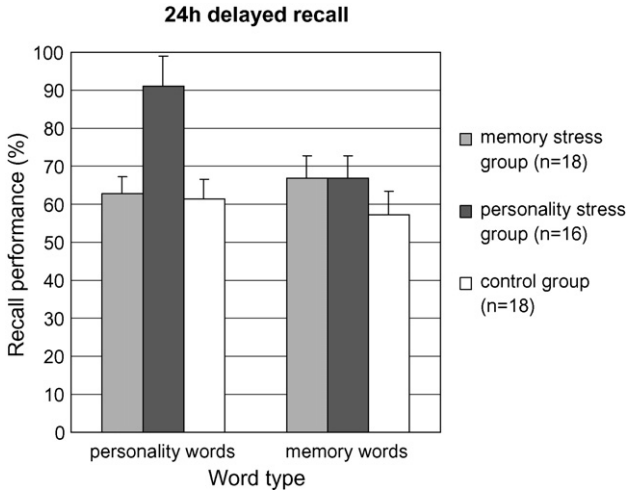

Fig. 4. Mean scores on the delayed free recall test controlled for immediate recall scores for the three groups. Error bars represent the standard error of mean (S.E.).

stress group (both rs $< .19$). For the memory stress group, cortisol and heart rate responses were not significantly related to recall of memory words or personality words (all rs $< .24$).

Delayed free recall performance controlled for immediate recall is shown in Fig. 4. ANOVA on these data confirmed our earlier analyses and yielded a significant main effect of group [$F(2, 49) = 4.45$; $p = .017$; $\eta_p^2 = .15$] in the absence of a significant effect of word type [$F(1, 49) = 2.49$; $p = .12$; $\eta_p^2 = .05$], while the critical group × word type approached significance [$F(2, 49) = 2.76$; $p = .07$; $\eta_p^2 = .10$]. Again, follow-up t-tests showed enhanced delayed recall of personality words in the personality stress group relative to the memory stress and no-stress control groups (both ps $< .02$).[3] Within-stress group correlations again showed that the only significant correlation was the correlation between cortisol responses and personality words ($r = .51$; $p < .05$) within the personality stress group.

3. Discussion

The main purpose of this study was to determine whether acute psychosocial stress would enhance declarative memory performance when the to-be-remembered material is context-congruent to the stressor. Results of the current study can be summarised as follows. Participants in both stress groups were significantly affected by the applied stressors (i.e., the modified versions of the TSST), as evidenced by the fact that both groups displayed significant heart rate responses and clear-cut cortisol increases following the TSST. Moreover, both groups reported increased feelings of subjective stress. As to the effects of acute stress on context-congruent and context-incongruent words, this is the first study to suggest that exposure to a stressor may improve memory for context-related declarative memory material. Participants in the personality stress group showed better delayed recall of personality-related words relative to controls and the memory stress group. In addition, in the personality stress group, cortisol stress responses were significantly related to correct recall of personality-related words. However, no memory-enhancing effect of contextual stress was noted for the memory-related words, with all groups showing similar levels of delayed recall.

One could speculate that the fact that our findings were limited to personality words was due to this set of words showing more semantic cohesion than memory words. However, the fact that there was no main effect of word type argues against such an interpretation. Another explanation would be that the context-congruency effect is highly specific and thus only applies to personality words. Alternatively, it could also mean that it reflects a general effect, but one that for some or the other reason does not apply to memory-related words. A third and perhaps most likely explanation would be that this effect is quite common but has certain limitations to it. For example, the reason that we found a convincing congruency effect for personality words, but not for memory words, might have to do with the specificity of the memory material congruency. That is to say, personality words are in a highly specific way congruent with the personality stress manipulation, yet memory words might have been considered relevant by all participants, as all of them were subjected to recall tests.

Of interest, pioneering work by Mason (1968) concluded that in stressful situations, ego threat was among the most potent causes of cortisol stress responses. Indeed, a recent meta-analysis showed that fear of negative social evaluation was closely related to cortisol increases as elicited by laboratory

[3] To check whether menstrual cycle phase or oral contraceptive use had an impact on our results, we repeated all analyses with these factors included as covariates. No discrepancies were found between the results with these covariates included and the results reported here. As previous research obtained evidence for sex differences involving cortisol effects on memory performance (e.g., Wolf et al., 2001), we ran additional ANOVAs to check whether sex modulated the current results. However, we found no evidence for a modulating role of sex, with all main and interactive effects involving sex yielding non-significant p-values.

stressors (Dickerson and Kemeny, 2004). Of course, ego threat or fear of negative social evaluation means that an individual has concerns about the fact that others might get an unfavorable impression of him/her as a person, i.e., of his/her personality. This is important as it implies that in the current study, personality words were very relevant to, and were highly associated with, the content of the concerns that provoked the cortisol increases in the personality stress group. The fact that personality stress enhanced recall of personality words but that recall of memory words was not affected by memory stress, therefore suggests that memory is enhanced only when the to-be-remembered stimuli are highly associated with the stimuli that provoke the cortisol stress responses (e.g., ego threat, personality descriptors used in the TSST).

Note, however, that in the present study ego threat was elicited by both the personality and the memory TSST. As Joëls et al. (2006) hypothesized that stress will induce focused attention and improve memory of contextually relevant over irrelevant information, one thus would have expected enhanced recall of personality words in both stress groups. Since recall of personality words was not enhanced in the memory stress group, additional assumptions are necessary to account for the current results. Hence, although personality words may not have been intrinsically ego threatening, they may have elicited social evaluative concerns and emotional arousal after being exposed to personality stress. In other words, the personality words may have reminded individuals in the personality stress group of their attempts to find and choose self-descriptive words in the social evaluative context. Perhaps, then, the TSST does not activate personality words. But when personality words are activated by the recall test, they are nevertheless easily associated with the social evaluative context, in contrast to memory words.

In any case, the present results suggest that there are limits to context-effects in the link between stress and enhanced declarative memory performance. Further research is needed to accurately define the precise conditions (i.e., the common characteristics between context and memory material) under which context may boost memory-enhancing effects of acute stress. Furthermore, future studies could also investigate whether these effects surface for non-declarative memory material like, for example, in fear inhibitory avoidance tasks that have been shown to be related to contextual fear conditioning (e.g., Grillon et al., 2004; Ji et al., 2003; LaLumiere et al., 2003).

Our finding that contextual stress may enhance declarative memory under certain circumstances ties in nicely with animal studies. These studies show that acute stress that is intrinsically related to a learning task facilitates consolidation of the event (e.g., de Kloet et al., 1999). Sandi (1997), for example, showed that in rats trained in a spatial memory task (i.e., Morris water maze task), GC elevations were positively related to spatial memory performance. The importance of GCs for effective learning and subsequent memory performance has also been shown in humans (e.g., Kuhlmann and Wolf, 2006; Lupien et al., 2002). Thus, the present findings as well as those of animal studies seem to converge on the notion that GC elevations within the context and around the time of the memory acquisition phase may exert beneficial effects on successive memory tasks. Note that we found a memory enhancing effect of stress for the delayed, but not the immediate recall test, suggesting that contextual stress primarily enhances the consolidation of context-congruent memory material rather than affecting the encoding phase. Indeed, our results are in line with work by Cahill et al., 2003 and Andreano and Cahill (2006) showing enhanced recall of memory material following consolidation stress.

An important modulator of the link between effects of acute stress and GCs and memory performance is the time of day when GCs are administered or stress is applied to participants. In general, research shows that GCs given in the morning hours tend to yield detrimental memory effects, while GCs given in the afternoon either have no effect or exert a small enhancing effect on memory. A good example comes from a recent study by Maheu et al. (2005). These authors had 19 young men watch a story after being subjected to a psychological stress task (i.e., stress group), while another 20 men did so without being exposed to a stressor (i.e., controls). Maheu et al. further divided both groups in either a morning group that saw the memory material in the morning or an afternoon group that saw it in the afternoon. When tested for their memory 1 week later, those participants who were stressed and had viewed the material in the morning, as compared to the afternoon stress group, showed impaired recall performance for emotional details of the memory material. The current study shows that these detrimental effects of early acute stress are not universal. After all, participants in the present study were exposed to the TSST in the morning and memory facilitatory effects were found for congruent memory material (i.e., personality words).

Note that our results may have some interesting implications for clinical practice. Specifically, when people are confronted with stressful situations, ego threat is assumed to be strongly related to stress and cortisol stress responses (Mason, 1968; cf. supra). This, in turn, could mean that exposure to stress or the ensuing cortisol stress reactions may have an increased impact on ego-related memory like, for example, in modulating, increasing and/or consolidating individuals' self-perception of low or high self-esteem. As people suffering from severe social anxiety are characterized by high cortisol responses in the context of high fear of negative social evaluation (e.g., Condren et al., 2002; Martel et al., 1999) and exposure to phobic stimuli is known to provoke the retrieval of stimulus-associated fear memory (Cuthbert et al., 2003), these stress reactions may be involved in the development, increase, and/or maintenance of social anxiety and avoidance of social situations that somehow have been associated with social evaluative threat (see also Soravia et al., 2006).

As to the limitations of this study, it can be argued that in contrast to free cortisol levels, heart rate data and subjective measures of affect (i.e., POMS) perhaps are not paramount markers for individuals' stress reactions. That is, heart rate is well known to increase under a variety of circumstances other than stress (e.g., task engagement, excitement, bodily movements, etc.). Similarly, the POMS is a general measure of affect

and thus might be sensitive to a host of manipulations. However, it should be noted that the heart rate and POMS increases obtained in the stress groups are in support of the present study's cortisol data.

In sum, the present study provides preliminary evidence that exposure to an acute psychosocial stressor may improve context-related declarative memory. Follow-up studies should further delineate the exact conditions under which context-dependent memory may be enhanced by acute psychosocial stress and determine its underlying neurobiological mechanisms.

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