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The effect of acute stress on memory depends on word valence

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Abstract

The present study investigated the effect of acute stress on working memory and memory for neutral, emotionally negative, and emotionally positive words in healthy undergraduates. Participants ($N=60$) were exposed to either the Trier Social Stress Test (stress group) or a non-stressful task (control group). Analyses of salivary cortisol samples taken throughout the study showed elevated glucocorticoid levels after the experimental manipulation in the stress group, but not in the control group. Recall performance was impaired in the stress group, but only so for neutral words. No differences between the stress and control group were found on working memory measures. For the stress group, digit span forward and digit span total scores were associated with correct recall of neutral words. All in all, this study lends further support to the notion that the memory effects of exposure to acute stress depend on the valence of the memory material.

Keywords: Acute stress; TSST; Cortisol; Stimulus valence; Verbal memory; Working memory

1. Introduction

A bulk of animal research has demonstrated that the secretion of glucocorticoids (GCs) from the adrenal cortex during stress may modulate memory storage and consolidation (e.g., de Kloet et al., 1999; McGaugh, 2000; Roozendaal, 2000). In animals, GCs can have facilitating (e.g., on aversive conditioning) as well as impairing effects on memory (e.g., de Kloet et al., 1999; Lupien and McEwen, 1997; McGaugh and Roozendaal, 2002). Similarly, studies in humans have shown that acute GC administration can have enhancing as well as disruptive effects on memory, depending on several modulatory variables (for reviews, see Het et al., 2005; Lupien and Lepage, 2001; Wolf, 2003). The effects of GCs on memory depend on the differential activation of both mineralocorticoid receptors (MR) and glucocorticoid receptors (GR). It appears that when high affinity MRs are fully occupied while GRs are only partially activated, memory can be facilitated. On the other hand, detrimental effects of high GC levels may occur when GRs become exceedingly saturated during stressful situations (e.g., de Kloet et al., 1999; Oitzl and de Kloet, 1992; Reul and de Kloet, 1985). Furthermore, adrenergic activation in the basolateral complex of the amygdala (BLA) and in the hippocampus seems to be required for GCs to impair retrieval (Roozendaal et al., 2004). Also, activation of noradrenergic mechanisms in the BLA may, in combination with several other brain regions including the hippocampus and prefrontal cortex, mediate the effects of emotional arousal in combination with GC effects on memory functioning (e.g., McGaugh and Roozendaal, 2002).

Previous research has shown that men and women not only differ in their endocrinological response to acute psychosocial stress (Kirschbaum et al., 1992; Kudielka and Kirschbaum, 2005), but also that the effects of acute stress and/or GC elevations can bring about memory effects that differ for men and women (e.g., Takahashi et al., 2004; Wolf et al., 2001; for review, see Wolf, 2003). In line with animal research (e.g., Roozendaal, 2002), GCs may exert differential effects on various memory phases. In particular, GCs are known to facilitate memory formation (e.g., Buchanan and Lovallo, 2001) while impairing retrieval (e.g., de Quervain et al., 2000; Wolf et al., 2004).

Additionally, prior research has shown that for humans, the effect of stress-induced GC secretion may be detrimental to declarative memory performance, while leaving implicit memory intact. Indeed, there have been studies (e.g., Abercrombie

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et al., 2003; de Quervain et al., 2000; Domes et al., 2005; Jelicic et al., 2004; Kirschbaum et al., 1996; Kuhlmann et al., 2005a; Lupien et al., 1997; Newcomer et al., 1994; Newcomer et al., 1999; Tops et al., 2003) illustrating the deleterious effects of acute stress and/or cortisol elevations on declarative memory performance. Kirschbaum and colleagues (1996), for example, found that impaired declarative memory performance was associated with strong cortisol responses following an acute psychosocial stressor (Experiment 1) and the administration of cortisol (Experiment 2).

Interestingly, some studies have reported that the effect of cortisol on memory performance might depend on the valence of the material being studied. Tops et al. (2003) showed that two hours after participants were given either 10 mg cortisol or placebo, those who had been given cortisol exhibited impaired recall and recognition of neutral and pleasant words, whereas no difference was found between both groups for unpleasant words. Using a more natural way to elicit high levels of cortisol, Jelicic et al. (2004) exposed half of their participants to a Trier Social Stress Test (TSST; Kirschbaum et al., 1993), which basically consists of a 5 min free speech followed by a 5 min mental arithmetic task, while the other half was given a non-stressful control task. Jelicic and colleagues (2004) found that participants in the stress condition exhibited enhanced recall of emotional words, but showed impaired recall of neutral words. In a study by Abercrombie et al. (2003), 90 men were administered either 20 mg or 40 mg of hydrocortisone or placebo and were later asked to rate a list of negative and neutral words for pleasantness and arousal. At a follow-up session 2 days later, Abercrombie et al. found evidence for an inverted U-shaped quadratic trend across stimulus valence, with memory facilitation for both neutral and negative words in the 20 mg hydrocortisone group. These results suggest that only moderate doses of hydrocortisone enhance memory for words, irrespective of the valence of the studied material.

Recently, Rimmele and co-workers (2003) had their participants view an emotionally arousing or a neutral story following the administration of 25 mg of hydrocortisone or a placebo. One week later, participants who were given cortisol exhibited enhanced memory for details of the neutral story version, but impaired memory for details of the emotional story. Using a word list containing neutral, pleasant, and unpleasant words, Domes et al. (2004) exposed participants to the TSST either before learning the word list or before retrieval, or were not stressed at all. While free recall was not affected by exposure to the TSST, recognition memory for positive words was impaired for participants who were stressed before retrieval. In a study by Kuhlmann et al. (2005b), healthy young males who had learned a word list including neutral, negative, and positive words 24 h earlier were either assigned to a stress (TSST) or a control condition. In a subsequent free recall task, participants in the stress condition showed impaired memory for the emotionally arousing, but not the neutral words. Most recently, Kuhlmann et al. (2005a) exposed sixteen healthy female participants to either 30 mg hydrocortisone or placebo after they had learned a list containing neutral and negative words. Kuhlmann et al. found that recall for negative words was most strongly impaired at a recall test 5 h later, while recall for neutral words only tended to be impaired.

In sum, then, results in this research domain on one hand seem to suggest that memory of neutral material is more disrupted by mild psychosocial stress and/or small to moderate cortisol increases (e.g., doses <20 mg cortisol) than is memory of emotionally provocative material. On the other hand, there have been some divergent findings (e.g., with regard to the effects of cortisol on positive material). One way to account for these divergent findings is to look at the effect of stress-induced cortisol on working memory. Recent studies suggest that impaired memory may – at least in part – be the result of post-stress variation in working memory performance (al' Absi et al., 2002; Lovallo and Thomas, 2000; Lupien et al., 1999). That is, high levels of GCs, resulting in occupancy of low-affinity GRs, have been shown to cause a temporary reduction in long-term potentiation (LTP), which in turn may account for post-stress decrements in working memory performance. Moreover, a recent study by Elzinga and Roelofs (2005) found that adrenergic activity is necessary for stress-induced cortisol elevations to impair working memory. The current study thus sought to replicate the finding that stress-induced cortisol increases interfere with memory of neutral material, but not with that of emotional material. We also expected that for the stress group, but not the control group, reduced working memory performance would be associated with impaired medium long-term memory performance.

2. Methods

2.1. Participants

Our sample consisted of 60 healthy undergraduate students (30 men and 30 women). Their mean age was 19.65 years (±0.24 (SE); range 17–28). Participants were asked whether they suffered from any cardiovascular diseases or endocrine disorders. If so, they were excluded from the study. All test protocols were approved by the local standing ethics committee of the Psychology Faculty of Maastricht University. All undergraduates participated voluntarily, gave written informed consent, and were paid 10 Euro for completing the experiment.

2.2. Materials

2.2.1. Profile of Mood States

Subjective stress was measured using the Anger–Hostility and Tension–Anxiety subscales of the Profile of Mood States — Short Form (POMS; McNair et al., 1992). The POMS is a self-report measure that is widely used as a 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 5-point scales (anchors: 0=*not at all*, 4=*extremely*). Adjectives include "annoyed", "angry", and "grumpy" for the subscale Anger–Hostility and "nervous", "tensed", and "panicky" for the Tension–Anxiety subscale. The POMS has excellent psychometric properties (see for example, Lezak, 2004c; McNair et al., 1992; Shacham, 1983).

The present experiment used a Dutch version of the POMS that has been proven to be both valid and reliable (de Groot, 1991; Wald and Mellenbergh, 1990).

2.2.2. Working memory testing: digit span

The digit span task (see Lezak, 2004b), a subtest of the Wechsler Adult Intelligence Scale — Revised (Wechsler, 1981), requires participants to listen to a series of numbers (ranging from 0 to 9) of increasing length that are read to them at a constant pace of one digit per sec. After the last digit has been presented, participants have to repeat the numbers in the exact same (forward condition) or the exact reverse (backward condition) order. On each successful attempt, the number of digits per list increases. Thus, the digit span involves auditory attention and depends on working retention capacity. Whenever a participant fails to reproduce a certain list of numbers, a second attempt with another list of digits of equal length follows. When a participant fails to accurately reproduce a list of numbers on two successive trials (e.g., failing to reproduce a 6-item list on two successive trials), the task ends. On average, people recall about 7 items (Miller, 1956). Raw scores for the digit span forward and backward reflect the maximum number of digits correctly recalled. Digit span forward and backward scores are summed to obtain a digit span total score.

2.2.3. Declarative memory testing: 30 word verbal learning task

The 30-word Verbal Learning Task (30WVLT) is an adapted version of the Rey Auditory Verbal Learning Task (originally published by Rey, 1964; also see Deelman et al., 1980; Lezak, 2004a) designed to assess learning capabilities, maximal and total capacity, and storage as well as retrieval efficiency of verbal material. Participants are required to listen to and remember as many words as possible from a list of 30 words, read out to them at a pace of one word every 2 s. As the valence of stimuli may differentially affect recall (e.g., Tops et al., 2003), the list of presented stimuli words comprised 10 positive emotional (e.g., "peace"), 10 negative emotional (e.g., "cancer"), and 10 neutral (e.g., "stone") words, all acquired early in life. All words were chosen from Hermans and De Houwer's (1994) list of words for which they had 352 first year students rate the subjective familiarity and affectivity of 740 Dutch words. Based on these data, all three word categories (positive emotional, negative emotional, and neutral) differed significantly for affectivity [$F(2,27)=1491.15$; $p<.0001$], but not for familiarity or word length ([$F(2,27)=1.91$; *ns*] and [$F(2,27)<1$; *ns*], respectively). Presentation order of the 30 words was randomized.[1] After the list had been read to participants, they were instructed to freely reproduce as many words as possible. However, they were not told that the list consisted of 30 words. Next, the 30 words were read out again and participants were required to reproduce them. After 3 such 'learning' trials had taken place, a retention interval of 30 min was maintained after which participants were given a delayed recall and recognition task. Recall performance was scored as the proportion correctly recalled positive, negative, and neutral words, with higher scores indicating superior correct recall performance. The recognition task consisted of 60 words (30 presented and 30 non-presented). The 30 new, non-presented words were also taken from Hermans and De Houwer (1994) and included 10 emotionally positive, 10 emotionally negative, and 10 neutral words. A one-way Analysis of Variance (ANOVA) showed that the 10 new positive emotional words did not differ significantly from the 10 old words that were presented in the word learning task with regard to affect, familiarity, or word length (all F's<1). Likewise, the old and new emotionally negative words did not differ in terms of affect, familiarity, or word length (all F's<2.5; all p's$>.10$). Neither were there differences between new and old neutral words (all F's<1). Order of old and new words in the recognition task was random. Recognition performance was assessed by calculating a Discrimination Index *Pr* (Snodgrass and Corwin, 1988). *Pr* indicates the ability to discriminate old from new words and was computed as follows: *Pr* = (hit rate – false alarm rate). Higher *Pr*'s are indicative of enhanced recognition performance.

2.3. Saliva sampling and free cortisol analysis

Cotton Salivettes (Sarstedt®, Nümbrecht, Germany) were used to obtain the cortisol samples. The uncentrifuged saliva samples were stored at −40 °C immediately upon collection. Salivary free cortisol levels were determined in duplicate by direct radioimmunoassay (RIA; University of Liège[2]), including a competition reaction between ^{125}iodohistamine–cortisol and anti-cortisol serum made against the 3-CMO-BSA conjugate. Via a conventional 'second antibody' method, separation of free and antibody-bound ^{125}iodohistamine–cortisol was performed after overnight incubation at 4 °C of 100 µl of saliva. In order to reduce sources of variability, all 4 samples from an individual were analyzed in the same assay. Mean intra- and inter-assay coefficients of variation were less than 4.3% and 8.3%, respectively.

2.4. Design

A 2-group between-subject design was employed. Half of the participants (i.e., 15 men and 15 women) were exposed to the TSST (Kirschbaum et al., 1993), while the other half were assigned to a non-stressful control group. The two groups did not differ with respect to age (stress group 19.47 ± 0.24 years (mean ± *SE*); control group 19.83 ± 0.40 years; [$t(58)<1$; *ns*]).

2.5. Procedure

All sessions were run between 14 and 17 h to obtain comparable and stable basal cortisol levels. All participants

[1] The list of stimuli words used in this experiment can be obtained from the corresponding author.

[2] The authors would like to thank Dr. José Sulon from the Department of Veterinary Medicine, University of Liège (Belgium), for conducting the cortisol analyses.

were tested individually. To allow for objective controlled cortisol sampling, participants refrained from food, drinks, smoking, and heavy exercise at least one hour prior to the test phase. Upon arrival in the laboratory, participants were informed about the nature and procedure of the experiment and signed a consent form. After a short rest period, a first cortisol sample (baseline; t_{-5}) was obtained using Salivettes and the POMS was administered a first time. In order to eliminate anticipatory stress reactions (e.g., Kirschbaum et al., 1992) which could affect baseline cortisol measurement, participants were told about the task they had to perform subsequently only after the baseline cortisol measurement had already been performed. Male and female participants were pseudo randomly assigned to either the stress or the control group. In the stress group, participants were exposed to the TSST (Kirschbaum et al., 1993). The TSST protocol basically consists of a 10 min preparation period, a 5 min free speech, and a 5 min mental arithmetic task in front of an audience while being videotaped. The TSST has repeatedly been shown to be a valid and reliable procedure to induce physiological stress responses in children, young as well as elderly adults (e.g., Kirschbaum et al., 1992; Kudielka et al., 2004a, b). Moreover, in a recent meta-analysis, the TSST was found to provoke the most robust physiological stress responses (i.e., cortisol stress responses) as compared to several other laboratory stress tasks (Dickerson and Kemeny, 2004). Participants in the control group were given a non-stressful filler task that consisted of filling out some questionnaires and playing a computer card game. The TSST and filler task had a similar duration.

Subsequent to the TSST or filler task, a second cortisol sample (t_{+15}) was obtained and the POMS was again administered. Afterwards, the 30 WVLT and digit span task were administered. During the 30 min retention interval for the delayed recall task of the 30WVLT, non-verbal filler tasks were given. A third (t_{+35}) and fourth (t_{+55}) cortisol sample were obtained 20 min after finishing the TSST and at the end of the test session, respectively. The total time of the experiment did not exceed 1 h. Finally, participants were debriefed, paid, and thanked for their participation.

2.6. Statistical analyses

Cortisol responses were analyzed using a 2(group) × 2(gender) × 4(time: t_{-5} vs. t_{+15} vs. t_{+35} vs. t_{+55}) Analysis of Variance (ANOVA) with time as repeated factor. A 2(group) × 2(gender) × 2(time: pre-test vs. post-test) ANOVA was used to check feelings of distress (POMS) following the TSST or filler task. Digit span performance was analyzed using 2(group) × 2(gender) ANOVA. Learning, recall, and recognition performance for the negative, neutral, and positive words were analyzed using 2(group) × 2(gender) × 3(valence: positive vs. negative vs. neutral) ANOVA's, with valence as repeated factor. Additionally, delta increases in cortisol (i.e., cortisol responses) defined as peak cortisol level (t_{+15}, t_{+35} or t_{+55}) minus baseline cortisol level were computed for each participant individually and correlated (Pearson correlations, two-tailed) with memory performance measures within the stress group. Finally, to investigate the role of working

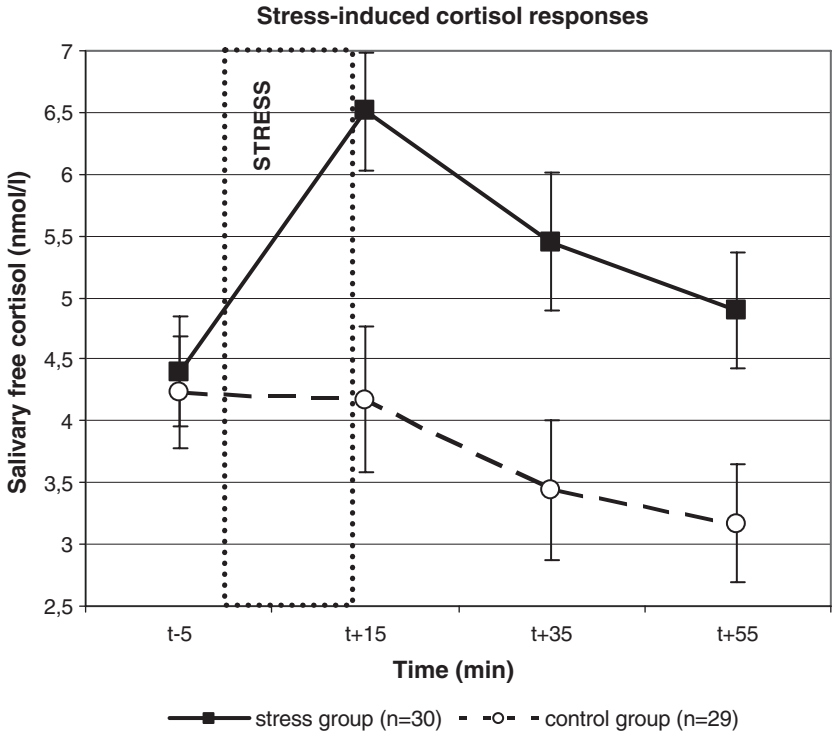

Fig. 1. Mean free salivary cortisol response (nmol/l) before stress manipulation (t_{-5}), directly after stress exposure (TSST; t_{+15}), 20min after stress exposure (t_{+35}), and at the end of testing (t_{+55}).

memory in acute stress effects on declarative memory performance, recall and recognition performance on the word learning task was correlated with digit span scores for the stress and control group separately (two-tailed). Alpha was set at .05 unless specified otherwise. When sphericity assumptions were violated, Greenhouse–Geisser corrected p-values are reported.

3. Results

3.1. Baseline cortisol analyses

Cortisol data from one female participant in the control condition was lost due to saliva sampling problems. An independent samples t-test showed no differences in baseline cortisol levels between the stress group and the control group, means being 4.40 nmol/l (±0.36 (*S.E.*)) and 4.26 nmol/l (±0.54), respectively [$t(57)<1$; *ns*].

3.2. Glucocorticoid stress responses

Repeated measures ANOVA revealed that salivary free cortisol levels were significantly higher in the experimental (i.e., stress) than in the control group, as indicated by main effects of time [$F(3,165)=6.69$; $p=.002$], group [$F(1,55)=6.04$; $p=.017$], and the critical Group × Time interaction [$F(3,165)=4.81$; $p=.011$]. No other main or interactive effects were found. Bonferroni corrected post hoc tests indicated that levels of cortisol were significantly higher in the stress group at t_{+15} [$t(57)=2.82$; $p=.007$], t_{+35} [$t(57)=2.53$; $p=.015$], as well as at t_{+55} [$t(57)=2.60$; $p=.013$]. Fig. 1 shows mean salivary cortisol levels throughout the experiment for both groups.

3.3. Psychological assessment of subjective stress

Mean scores on the POMS subscales Anger–Hostility and Tension–Anxiety are shown in Table 1. As to the Anger–Hostility subscale scores, significant main effects of group [$F(1,56)=6.18$; $p=.016$], time [$F(1,56)=4.15$; $p=.046$], and the crucial Group × Time interaction [$F(1,56)=4.84$; $p=.039$] were found, in the absence of other main or interactive effects. Similarly, significant effects of group [$F(1,56)=12.64$; $p=.001$], time [$F(1,56)=10.78$; $p=.002$], and the Group × Time interaction [$F(1,56)=31.00$; $p<.001$] were observed for Tension–Anxiety subscale scores. These differences indicate that experimental participants experienced significantly more stress than control participants.

Table 1
Mean scores on subscales Anger–Hostility (AH) and Tension–Anxiety (TA) of the Profile of Mood States before (Pre-AH and Pre-TA) and after (Post-AH and Post-TA) the experimental manipulation

	Pre-AH	Post-AH	Pre-TA	Post-TA
Control group	0.90 (0.30)	0.87 (0.35)	5.53 (0.39)	4.73 (0.42)
Stress group	1.63 (0.70)	3.37 (0.72)	5.43 (0.49)	8.53 (0.45)

Standard errors of mean are given between parentheses.

Table 2
Mean scores on Digit Span Forward (DS-FW), Backward (DS-BW), and Total, and mean recall and recognition performance (*Pr*) for neutral, positive, and negative words for the stress and control group

	Control group	Stress group
Digit Span		
Forward condition	6.83 (0.28)	6.83 (0.19)
Backward condition	5.70 (0.28)	5.63 (0.23)
Total score	12.53 (0.51)	12.47 (0.33)
Mean percentage correct recall		
Neutral words	.72 (0.02)	.60 (0.03) *
Positive words	.63 (0.03)	.63 (0.03)
Negative words	.74 (0.03)	.69 (0.04)
Mean number of commissions	0.27 (0.15)	0.70 (0.14) **
Mean recognition performance (Pr)		
Neutral words	.99 (0.01)	.91 (0.02) *
Positive words	.94 (0.02)	.91 (0.03)
Negative words	.92 (0.01)	.86 (0.03)

Standard errors of mean are given between parentheses.
* $p<0.01$, two-tailed.
** $p<0.05$, two-tailed.

3.4. Memory performance

3.4.1. Digit span

Descriptive results on digit span measures can be found in Table 2. For digit span forward, ANOVA revealed a main effect of gender [$F(1,56)=6.45$; $p=.014$], but not of group [$F(1,56)<1$; *ns*], with men having slightly higher digit span forward scores than did women. The Group × Gender interaction just fell short of significance [$F(1,56)=3.63$; $p=.06$]. No main effect of group or gender, or a Group × Gender interaction was found for digit span backward (all F's<1; *ns*).

3.4.2. Word learning task — recall performance

Learning performance as measured by overall proportion of recalled words after each learning trial did not differ between groups at learning trial 1 (means being .40 and .41 for the stress and control group, respectively; [$F(1,56)<1$; *ns*]), learning trial 2 (means being .59 and .60 for the stress and control group, respectively; [$F(1,56)<1$; *ns*]), or learning trial 3 (means being .72 and .74 for the stress and control group, respectively; [$F(1,56)<1$; *ns*]). No other main or interaction effects were found in learning performance (all F's<1).

Mean percentage correctly recalled words for the delayed recall task can be found in Table 2. ANOVA yielded a significant main effect of valence [$F(2,56)=8.23$; $p<.001$] and a significant Group × Valence interaction [$F(2,56)=3.74$; $p=.03$]. No other main or interactive effects were detected. Bonferroni corrected post hoc analyses showed that recall of neutral words was significantly impaired in the stress group ($p<.01$), while no such impairment was found for negative or positive words (both p's$>.05$). Furthermore, we observed that the stress group made more list intrusions or commission errors (i.e., non-presented words being recalled) than the control group, [$F(1,56)=4.52$; $p<.05$].

3.4.3. Word learning task — recognition performance

As to recognition performance (*Pr*), ANOVA showed significant main effects of group [$F(1,56)=4.15$; $p<.05$] and

valence [$F(2,56)=6.70$; $p=.002$] in the absence of other main or interactive effects (all p's$>.10$). Bonferroni corrected post hoc analyses showed that the control group had higher discrimination indices than the stress group.

3.4.4. Correlations between digit span and recall and recognition performance on the word learning task

Correlations between digit span forward, backward, and total scores and recall and recognition performance for positive, negative, and neutral words were computed. For the stress group, this yielded significant correlations between correct recall of neutral words and digit span forward and total scores ($r=.41$; $p<.05$ and $r=.36$; $p<.05$, respectively). For the control group, no meaningful correlations emerged (all r's$<.30$; all p's$>.10$).

3.4.5. Within stress group correlations between memory performance measures and individual delta cortisol responses[3]

Delta cortisol responses were negatively related to digit span backward scores ($r=-.39$; $p=.03$). All other correlations remained non-significant (all p's$>.05$).

4. Discussion

The present study was set out to further evaluate effects of acute stress on declarative memory performance reported in previous studies (e.g., Kirschbaum et al., 1996) and the precise role of word valence in these effects (e.g., Tops et al., 2003). The main results of our study can be summarized as follows. Participants in the stress group did not differ from controls with respect to digit span measures. They did, however, show impaired recall of neutral words in the absence of learning differences between both groups. No differences between the groups were found for recall of positive emotional or negative emotional words. Additionally, participants in the stress group made more commission errors than did control participants. The recognition test showed that participants in the stress group performed worse than those in the control group. Moreover, in the stress but not the control group, post-stress performance on forward and total digit span was significantly correlated with correct recall of neutral words.

The finding that memory for neutral words was impaired for stressed participants accords well with previous findings obtained by Kirschbaum et al. (1996), Lupien et al. (1997), Wolf et al. (2001), Jelicic et al. (2004), and Tops et al. (2003). In contrast to the work by Buchanan and Lovallo (2001) and Jelicic et al. (2004), however, cortisol alterations in this study did not lead to enhanced memory for positive or negative emotional words. Note, however, that the cortisol levels reported by Buchanan and Lovallo were much higher than those reported here, due to the exogenous administration of high doses of cortisol. Also, these results are at odds with findings suggesting impaired memory for emotional material (e.g., Domes et al., 2004; Kuhlmann et al., 2005a,b; Rimmele et al., 2003). It should be acknowledged here that for recognition performance, the crucial interaction between group and valence remained non-significant despite significant effects of group and valence. This suggests that recall and recognition tasks may yield qualitatively different interaction effects between exposure to acute stress and the valence of the memory material.

In addition to the memory impairing effect of acute stress on memory for neutral words, we found that participants in the stress group committed significantly more commission errors during free recall. This is in accordance with findings from Wolkowitz et al. (1990), who reported that participants exposed to 80 mg/day of prednisone for 5 consecutive days made more commissions in a verbal memory task than participants who had received a placebo.

The present study failed to find differences between the stress and control group on digit span performance. Our data thus replicate the findings of Hoffman and al' Absi (2004) and Kuhlmann et al. (2005b), who reported no effects of acute stress on digit span performance. It should be noted here that Elzinga and Roelofs (2005) recently found that adrenergic activity is essential for cortisol elevations to result in working memory deficits. These results might explain why in the present study no impairments in working memory performance were noted despite the fact that cortisol levels were significantly elevated. However that may be, the current data do confirm our hypothesis that working memory performance following acute stress is associated with medium long-term memory performance. This association was evident for the stress group, while no such association was found for the controls. However, the fact that stress and control group did not differ in digit span or learning performance makes it impossible to confidently assert that post-stress variation in working memory performance adds to the observed memory effect.

Some notes on the limitations of this study are in order. First of all, although the stressed group showed significant increases in cortisol, it might be argued that levels of cortisol in the stressed group were insufficiently high to bear relevance to high levels of cortisol under circumstances of real-life stress. Secondly, it can be argued that the current study relied only on a limited number of memory measures, thereby failing to raise the matter of medium long-term memory versus long-term memory effects following acute psychosocial stress. Therefore, the effect of acute cortisol elevations on memory over longer delays (e.g., several weeks) awaits to be determined. Also, it should be acknowledged that for the female participants, cortisol responses may have been influenced by menstrual cycle and the use of oral contraceptives (Kirschbaum et al., 1992). It is also worthy of note that previous research has shown that GCs may differentially affect the various memory phases. That is, while GCs have been shown to enhance memory formation (e.g., Buchanan and Lovallo, 2001), impairments in retrieval have also been reported (e.g., de

[3] To further evaluate whether cortisol levels had a modulating effect on the present data, we conducted 3(Group: controls vs. low responders vs. high responders) × 2(gender) ANOVA's on our dependent (i.e., memory performance) measures. Results were similar to those reported in Sections 3.4.1 3.4.2 and 3.4.3., suggesting that cortisol levels do not modulate the current study's results.

Quervain et al., 2000; Wolf et al., 2004). Roozendaal (2002) suggests that the BLA under stressful circumstances turns the brain into a memory-consolidation state, while concurrently destabilizing future retrieval attempts. This could be important given the fact that the present study involved only one session. Indeed, strictly from a theoretical viewpoint, memory-facilitating effects of moderate GC increases on memory formation might even suppress or eliminate the detrimental effects of such GC's on retrieval processes. However, in the present study this would have been rather unlikely given the fact that no differences in learning performance were observed. Another factor that should be taken into account is that cortisol appears to lead to impairing effects when studies are conducted in the morning, while no or slightly enhancing effects are found in the afternoon (e.g., Het et al., 2005; Lupien et al., 2002). Therefore, it awaits to be seen whether the present results can be generalized to other times of day. Future research should take these limitations into account.

In sum, then, the present data lend further support to the idea that valence of the memory material modulates the effects of acute stress on declarative memory performance. Our results also suggest that even acute exposure to heightened levels of cortisol may under some circumstances result in pertinent impairments in memory for neutral material, but that emotional material seems relatively immune to the memory undermining effects of heightened cortisol. Future studies should further delineate the precise boundaries of this effect and explore whether certain modulating factors (e.g., retention delay, age) may account for the inconsistent findings in this research domain. Research into acute stress effects may help us to advance our understanding of the complex role GCs and stimulus valence play in the regulation of human memory functioning.

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