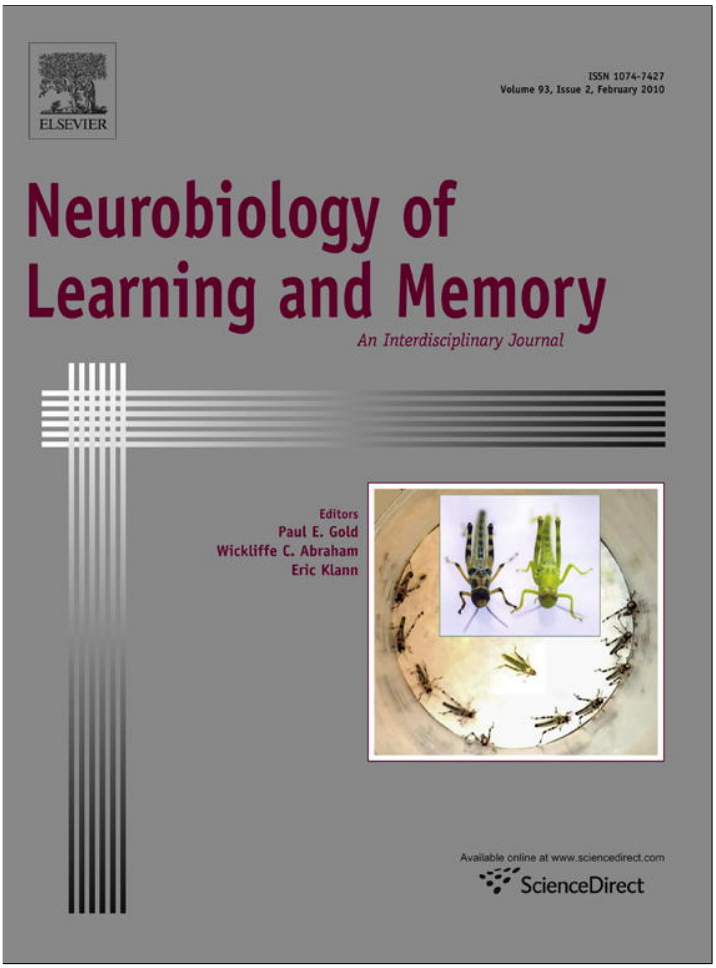

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Learning under stress impairs memory formation

Lars Schwabe *, Oliver T. Wolf

Department of Cognitive Psychology, Ruhr-University Bochum, Universitaetsstrasse 150, 44780 Bochum, Germany

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ABSTRACT

Converging lines of evidence indicate that stress either before or after learning influences memory. Surprisingly little is known about how memory is affected when people learn while they are stressed. Here, we examined the impact of learning under stress in 48 healthy young men and women. Participants were exposed to stress (socially evaluated cold pressor test) or a control condition while they learned emotional words and neutral words that were either conceptually associated with or unrelated to the stressor. Memory was assessed in free recall and recognition tests 24 h after learning. Learning under stress reduced both free recall and recognition performance, irrespective of the emotionality and the stress context relatedness of the words. While the effect of stress was comparable in men and women, women outperformed men in the free recall test. These findings show a memory impairing effect of learning under stress in humans and challenge some assumptions of current theories about the impact of stress around the time of learning on memory formation.

1. Introduction

Stress and the hormones and neurotransmitters released in response to stress, such as glucocorticoids and catecholamines, shape memory processes. The nature of these effects is time-dependent. Stress prior to learning can facilitate or reduce memory (Elzinga, Bakker, & Bremner, 2005; Payne et al., 2006; Schwabe, Bohringer, Chatterjee, & Schachinger, 2008). Stress immediately after learning enhances memory (Cahill, Gorski, & Le, 2003; Roozendaal, 2000; Wolf, 2008) whereas stress shortly before testing has mainly detrimental effects on memory (Buchanan, Tranel, & Adolphs, 2006; de Quervain, Roozendaal, & McGaugh, 1998; Schwabe & Wolf, 2009).

A recent model (Joels, Pu, Wiegert, Oitzl, & Krugers, 2006) explains these seemingly discrepant effects of stress by the biphasic effects of stress hormones, in particular glucocorticoids (GC; cortisol in humans, corticosterone in rodents). GC exert their effects via rapid non-genomic or delayed genomic pathways (de Kloet, Karst, & Joels, 2008). Joels and colleagues (2006) argue that early stress responses, including corticotropin releasing factor (CRF), noradrenaline and rapid GC actions favor attentional processes and the encoding of relevant information. Delayed genomic GC actions, however, would suppress neuronal activity and therefore reduce the processing of new information. Thus, it is assumed that stress enhances memory when it is experienced in the context and around the time of learning; stress out of the learning context is supposed to impair memory. Support for this model comes mainly from rodent studies. For instance, rats trained at a relatively low temperature of 19 °C, i.e. under very stressful conditions, in the Morris water maze showed better acquisition and retention rates compared to rats trained at 25 °C (Sandi, Loscertales, & Guaza, 1997). Moreover, synaptic plasticity in the rodent hippocampus is enhanced when high corticosterone concentrations coincide with repetitive stimulation while synaptic plasticity is impaired when corticosterone is administered before or after stimulation (Diamond, Campbell, Park, Halonen, & Zoladz, 2007; Kim & Diamond, 2002; Wiegert, Joels, & Krugers, 2006).

Comparable evidence from humans is largely missing. Only two very recent studies aimed to test the assumptions of the model by Joels and colleagues (2006) in humans (Smeets, Giesbrecht, Jelicic, & Merckelbach, 2007; Smeets et al., 2009). In these studies, participants were exposed to psychosocial stress shortly before they learned words that were either related or unrelated to the stressor. Corroborating the assumptions of Joels et al. (2006), stressed participants remembered more stressor-related words than non-stressed controls. In these studies learning took place after a 15-min stressor, i.e. when cortisol concentrations were already elevated. Whether learning under stress, i.e. at the onset of stress, when catecholamines and CRF rise but cortisol concentrations are not yet increased may enhance subsequent memory in humans is unknown.

In the present experiment, we examined the impact of stress during learning on memory performance. To this end, we presented participants information while they were exposed to stress (socially evaluated cold pressor test) or a control condition. The presented information varied in its emotionality from neutral to positive and negative because previous studies suggested that emotional material is particularly sensitive to the effects of stress

* Corresponding author. Fax: +49 234 3214308.
E-mail address: Lars.Schwabe@rub.de (L. Schwabe).

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(Buchanan et al., 2006; Kuhlmann, Piel, & Wolf, 2005). Furthermore, we presented material that was related to the stress context. Memory was assessed 24 h after learning. According to the model by Joels and colleagues (2006), it can be predicted that learning under stress enhances memory, in particular for stress context-related information.

2. Materials and methods

2.1. Participants and general procedure

Forty-eight healthy young men and women recruited at the Ruhr-University Bochum participated in this study (16 men, 32 women; age: $M = 23.6$ years, range 19–39 years; body-mass-index (BMI): $M = 22.4$ kg/m^2, range 18–28 kg/m^2). Twenty women were taking oral contraceptives. Exclusion criteria were checked in a standardized interview and comprised smoking, any medical illness within the prior 3 weeks, current or lifetime psychopathology, current treatment with psychotropic medications, β-blockers or steroids. Moreover, participants were asked to refrain from excessive exercise, meals and caffeine within the 2 h prior to the experimental sessions. Before the start of the study, all participants provided written informed consent to the study procedure as approved by the ethics committee of the German Psychological Association. Participants received either course credits or 15 € for participation.

All testing took place in the morning between 8 am and 1 pm to control for the diurnal variation of the stress hormone cortisol. On day 1, participants heard a list of eight neutral words that were related to the stressor as well as eight negative, eight positive and eight neutral, stressor-unrelated words while they were exposed to stress or a control condition (for details see below). On the following day, participants returned to the laboratory and completed a free recall and a recognition test for the words they heard the day before.

2.2. Stress protocol and control condition

After participants' arrival at the laboratory, they were randomly assigned to the stress or control condition (8 men and 16 women per group). Participants in the stress condition were exposed to the socially evaluated cold pressor test (SECPT) as described in detail elsewhere (Schwabe, Haddad, & Schachinger, 2008). Briefly, participants immersed their right hand up to and including the wrist for 3 min into ice water (0–2° C). During hand immersion they were videotaped, asked to look into the video camera and told that these video recordings would be analyzed later for facial expression. Furthermore, participants were monitored by a rather cold and unsociable experimenter. The SECPT has been used in several earlier studies as an efficient method to induce stress (Schwabe, Bohringer, & Wolf, 2009; Schwabe et al., 2009; Schwabe & Wolf, 2009b).

Participants in the control condition immersed their right hand up to and including the wrist into warm water (35–37° C). They were neither monitored nor videotaped.

Subjective stress ratings, blood pressure and salivary cortisol were measured to verify the efficacy of the SECPT.

2.2.1. Subjective stress ratings

Immediately after participants took their hand out of the water they rated on a scale from 0 ("not at all") to 100 ("very much") how stressful, painful and unpleasant they had experienced the previous situation.

2.2.2. Blood pressure measurements

Blood pressure was measured five times within 5 min immediately before (pre) and after (post) the SECPT or control condition as well as three times during hand immersion (values averaged per time point of measurement) using the Dinamap system (Critikon, Tampa, Florida) with the cuff placed at the left upper arm.

2.2.3. Salivary cortisol

Saliva samples were collected using Salivette (Sarstedt) collection devices at the beginning of the experiment on day 1, 25 min after the cessation of the SECPT or control condition when peak cortisol levels were expected (Schwabe, Haddad, et al., 2008) and before memory testing on day 2 to make sure that groups did not differ in their cortisol concentrations at test. Saliva samples were kept at −20° C until analyses. Free cortisol concentrations were measured from saliva using an immunoassay (IBL). Inter and intraassay coefficients of variance were below 10%.

2.3. Learning under stress

About 10 s after the beginning of the stress or control condition, participants were presented 32 words via headphones. They were told beforehand that they will be presented words and that they should try to memorize them. The auditory word presentation lasted 2 min and was thus finished prior to the end of the stress or control condition.

2.3.1. Word material

During the SECPT and the control condition, participants heard 32 German two-syllable nouns via headphones: eight neutral nouns that were related to the SECPT procedure (e.g. water, cold; in the following referred to as *context words*) as well as eight neutral (e.g. square, ink), eight positive (e.g. love, party) and eight negative (e.g. poverty, accident) nouns that were unrelated to the stress context. Word order was randomized.

Words were chosen from a German word database (Hager, 1994). To make sure that the presented words were really experienced as neutral, positive and negative, respectively, participants rated the words with respect to their valence and arousal on a scale from −3 ("negative"/"not at all arousing") to 3 ("positive"/"very arousing") following the recognition test on day 2. In retrospect, participants ratings confirmed that negative words ($M = -2.2$, SEM = 0.1) were experienced as significantly more negative than neutral words ($M = 0.0$, SEM = 0.1; context words: $M = -0.2$, SEM = 0.1) which were experienced significantly less positive than positive words ($M = 1.8$, SEM = 0.1; all $p < .01$). Negative words ($M = 0.9$, SEM = 0.2) were rated as most arousing; positive words ($M = -0.2$, SEM = 0.2) were rated as more arousing than neutral words ($M = -1.2$, SEM = 0.1; context words: $M = -1.1$, SEM = 0.1; all $p < .01$). Importantly, participants of the stress and control groups did not differ in their valence and arousal ratings (all $p > .20$).

2.4. Memory testing 24 h after learning

Twenty-four hours after learning, participants returned to the laboratory and completed a free recall test. They were instructed to write all words they could remember from the learning session on the day before on a sheet of paper. There was no time limit for the free recall test but all participants finished within 5 min.

Immediately after the free recall test, participants were given a recognition test. They saw a list of 64 words, including the 32 words they heard in the learning session as well as 32 new words (eight positive, eight negative, eight neutral and eight stress context-related two-syllable nouns), and had to indicate whether they remembered hearing the word on the previous day. To assess the participants' ability to discriminate between previously presented and new words we used signal detection theory parameters hit (i.e. correct identification of a previously presented word), false alarm (i.e. misclassification of a new word as previously presented) and

the sensitivity index d' (computed as $z[p\,(\text{hit})] - z[p\,(\text{false alarm})]$; see Wickens, 2002).

2.5. Statistical analyses

In order to examine the possible interactions between stress, sex and word category, memory data were subjected to group (stress vs. control condition) × sex × word category (positive vs. negative vs. neutral vs. context words) ANOVAs. Blood pressure and salivary cortisol changes in response to stress were analyzed by group × sex × time (time points of measurement) ANOVAs, stress effects on subjective assessments by group × sex ANOVAs. Significant main effects were further analyzed using Bonferroni adjusted post hoc tests where appropriate. All calculations were done with SPSS-statistical package (version 15.0; SPSS Inc.). Reported p-values are two-tailed. $p < .05$ was accepted as statistical significance. Analyses include the partial η^2 as measure of effect size. Following the conventions by Cohen (1988) partial $\eta^2 = 0.01$ is considered a small effect, partial $\eta^2 = 0.06$ a medium sized and partial $\eta^2 = 0.14$ a large effect.

3. Results

3.1. Subjective and physiological stress responses

Participants' subjective assessments, blood pressure and cortisol changes indicated the successful stress induction by the SECPT.

3.1.1. Subjective stress ratings

As expected, participants of the SECPT group experienced the hand immersion as significantly more stressful, painful and unpleasant than participants of the control group (all $F(1, 44) > 45$, all $p < .001$, all $\eta^2 > 0.50$, see Table 1). At a descriptive level, men assessed the SECPT condition as less stressful, painful and unpleasant than women, however this trend did not reach statistical significance (sex effect and group × sex effect: all $F(1, 44) < 3.5$, all $p > .07$, all $\eta^2 < 0.06$).

3.1.2. Blood pressure responses

The SECPT elicited significant elevations in systolic and diastolic blood pressure, while the control condition did not. As shown in Table 1, groups differed in systolic and diastolic blood pressure during but neither before nor after the stress and control condition, respectively (group × time effect: both $F(2, 88) > 20$, both $p < .001$, both $\eta^2 > 0.32$; time effect: both $F(2, 88) > 50$, both $p < .001$, both $\eta^2 > 0.54$; group effect: both $F(1, 44) < 1$, both $p > .40$, both $\eta^2 < 0.02$). Overall, men had higher systolic blood pressure than women (group effect: $F(1, 44) = 8.3$, $p < .01$, $\eta^2 = 0.16$; for diastolic blood pressure: $F(1, 44) = 0.6$, $p = .44$, $\eta^2 = 0.01$) but sexes did not differ in their blood pressure responses to the SECPT (group × sex and group × sex × time effect: all $F < 1$, all $p > .60$, all $\eta^2 < 0.01$).

Table 1
Subjective stress ratings and blood pressure values before (pre), during and after (post) the socially evaluated cold pressor test (SECPT) or control condition.

	Control condition		SECPT	
	Men	Women	Men	Women
Subjective assessments				
Stressfulness	10.0 (5.0)	8.1 (2.5)	44.8 (7.5)	58.0 (5.9)
Unpleasantness	13.8 (7.1)	6.9 (3.8)	49.3 (9.8)	64.6 (6.5)
Painfulness	1.3 (1.3)	0.6 (0.6)	48.6 (9.9)	65.3 (6.5)
Systolic blood pressure (mm Hg)				
Pre	121.9 (4.8)	109.8 (2.8)	118.6 (4.8)	109.7 (2.6)
During	123.6 (5.5)	113.0 (2.9)	137.2 (7.1)	125.2 (3.2)
Post	115.7 (4.8)	105.1 (2.1)	110.3 (4.1)	105.8 (2.4)
Diastolic blood pressure (mm Hg)				
Pre	68.1 (3.2)	66.2 (1.6)	65.8 (3.0)	63.2 (2.3)
During	70.8 (3.8)	67.4 (2.0)	77.9 (3.4)	77.1 (2.5)
Post	65.6 (3.1)	64.5 (1.3)	63.9 (1.7)	62.7 (1.8)

Stressfulness, unpleasantness and painfulness were rated on a scale from 0 ("not at all") to 100 ("very much"). Data represent means and SEM (in brackets).

3.1.3. Cortisol responses

Salivary cortisol concentrations increased in response to the SECPT but not in response to the control condition (group × time effect: $F(1, 44) = 14.9$, $p < .001$, $\eta^2 = 0.25$; time and group effects: both $F(1, 44) < 1.3$, both $p > .25$, both $\eta^2 < 0.03$; Fig. 1). Immediately before memory testing on day 2, cortisol concentrations were comparable in stressed and control participants ($t(46) = 0.81$, $p = .42$). Men and women differed neither in their cortisol responses to stress nor in their cortisol concentrations at test (all $p > .28$). Women taking oral contraceptives had overall lower cortisol concentrations than women not taking oral contraceptives (10.1 vs. 17.2 nmol/l; $F(1, 28) = 8.1$, $p < .01$, $\eta^2 = 0.23$) but oral contraceptive use did not change the cortisol response to stress (group × oral contraceptive use and group × time × oral contraceptive use: both $F(1, 28) < 1$, both $p > .30$, both $\eta^2 < 0.04$). Furthermore, the cortisol response to stress was not associated with the time of the stress exposure ($r = 0.12$, $p = .46$).

3.2. Memory performance 24 h after learning

Learning under stress reduced both free recall and recognition performance 24 h after learning.

3.2.1. Free recall performance

Participants who learned the words while they were stressed remembered significantly less words compared to participants who learned the words during the control condition (5.0 vs. 7.3 remembered words; $F(1, 44) = 6.1$, $p = .017$, $\eta^2 = 0.12$; see Fig. 2). This stress-induced memory impairment was neither influenced by participants' sex nor by the word category (both $F < 1$, both $p > .60$, both $\eta^2 < 0.01$). Yet, memory performance differed significantly for the four word categories ($F(3, 132) = 12.1$, $p < .001$, $\eta^2 = 0.22$): All participants remembered context words (i.e. words that were related to the treatment) best and negative as well as positive words better than neutral words (all corrected $p < .05$). In addition, women remembered significantly more words than men ($F(1, 44) = 5.8$, $p = .02$, $\eta^2 = 0.12$), irrespective of word category (sex × word category: $F(3, 132) = 0.7$, $p = .69$, $\eta^2 = 0.01$). Free recall performance did not correlate with the cortisol response to stress (all $r < .15$; all $p > .44$).

3.2.2. Recognition performance

Recognition memory as expressed by the discrimination index d' was impaired when participants were stressed during learning (1.13 vs. 1.67; $F(1, 44) = 4.1$, $p < .05$, $\eta^2 = 0.08$; Fig. 3). Neither the word category nor participants' sex modulated this effect of stress (all $F(3, 132) < 1$, all $p > .70$, all $\eta^2 < 0.01$). Fig. 3 shows that performance tended to be overall better for negative and context words than for positive and neutral words, this trend however was not reliable ($F(3, 132) = 2.3$, $p = .09$, $\eta^2 = 0.05$). Men and women were similar in their recognition memory ($F(1, 44) = 1.9$, $p = .17$, $\eta^2 = 0.04$). There was no correlation between recognition memory and cortisol response to stress (all $r < .17$, all $p > .10$).

4. Discussion

Earlier human studies examined changes in memory when participants were stressed before learning, after learning or before

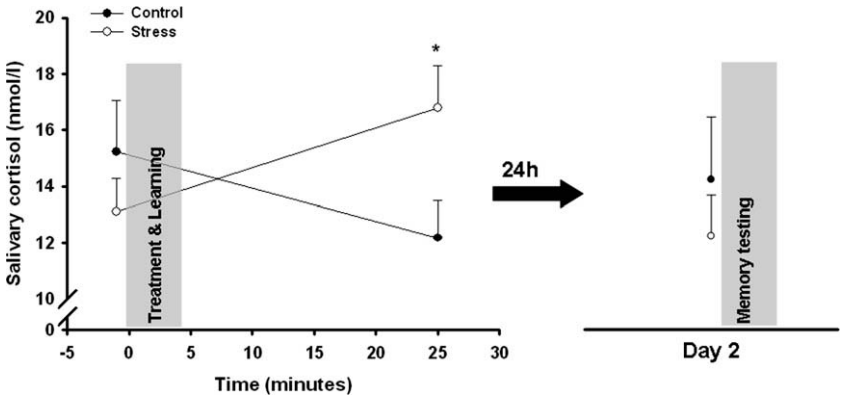

Fig. 1. Salivary cortisol concentrations in the stress and control groups. The SECPT but not the control condition caused a significant increase in cortisol. Groups had similar cortisol concentrations before retention testing on day 2. *Significant group difference ($p < .05$). Data represent means ± SEM.

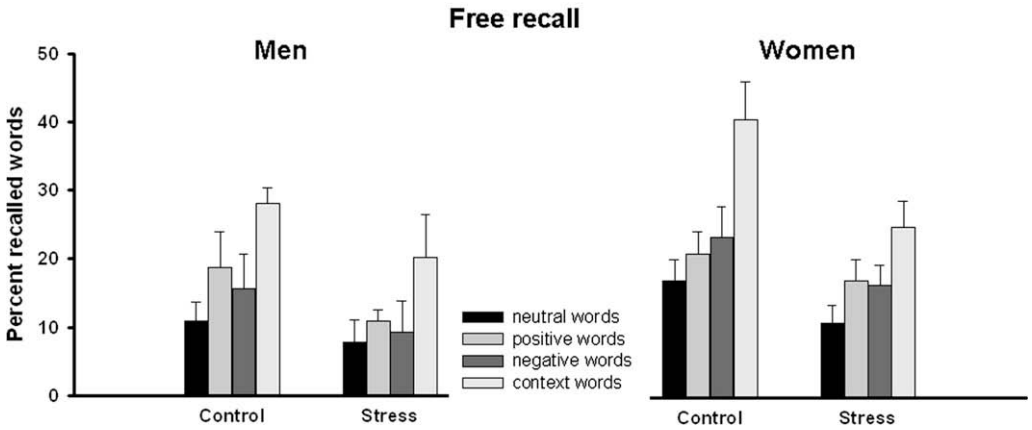

Fig. 2. Free recall 24 h after learning. Memory performance was significantly impaired in participants who learned under stress. Words that were related to the stress context were best remembered. Women remembered more words than men. Data represent means ± SEM.

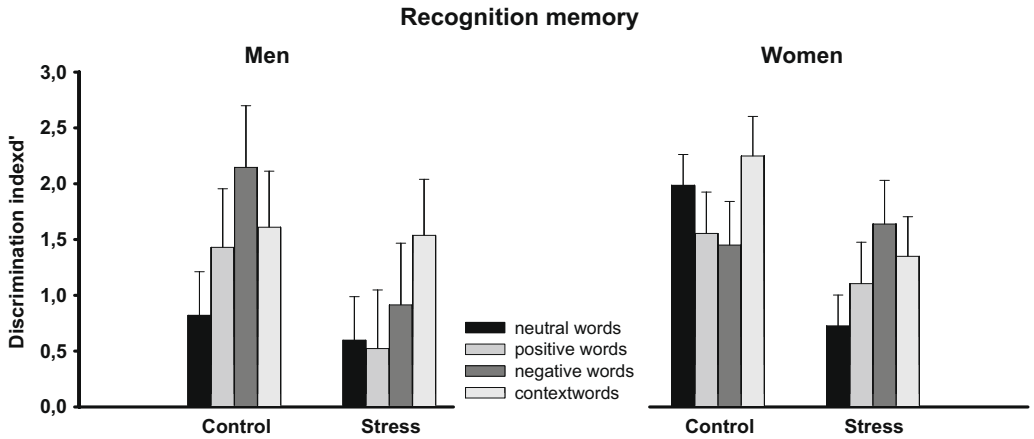

Fig. 3. Recognition memory 24 h after learning expressed as discrimination index d' (d' = 3.57 would indicate perfect recognition memory). Stress during learning impaired performance. Data represent means ± SEM.

retention testing (Joels et al., 2006; Wolf, in press). To our knowledge, the present study is the first that assessed the impact of learning under stress, i.e. at the onset of the stress response. Our results show profound memory impairment in participants that were stressed during learning. Learning under stress reduced both free recall and recognition performance by more than 30%. This detrimental effect of stress appeared to be independent of the learned material. It was found for neutral and emotional information as well as for stressor-related and stressor-unrelated information.

The obtained memory impairment might be potentially due to stress effects on memory encoding or consolidation. However, we consider the latter alternative very unlikely because there is a good deal of convincing evidence from human and animal studies that stress facilitates memory consolidation (Cahill et al., 2003; McGaugh, 2000; Roozendaal & McGaugh, 1997; Wolf, 2008). Thus, we suggest that stress affected primarily encoding processes. At a neural level, this encoding deficit might by owing to a stress-induced hippocampal deactivation (Khalili-Mahani, Dedovic, Engert,

Pruessner, & Pruessner, in press; Pruessner et al., 2008). Importantly, the stress effect on encoding could not be mediated via cortisol since glucocorticoids are secreted with a delay of several minutes after stressor onset but rather via neurotransmitters such as dopamine or noradrenaline. This view receives some support by the absence of a correlation between cortisol and memory in the present study and by previous findings showing impaired memory encoding following treatment with a noradrenaline reuptake inhibitor (Papps, Shajahan, Ebmeier, & O'Carroll, 2002).

At first glance, our findings appear to be in sharp contrast to the model proposed by Joels and colleagues (2006). These authors suggest that stress around the time of learning enhances memory; here we report clear memory impairment in individuals who learned while they were stressed. In addition to the timing of stress, however, there is according to Joels et al. (2006) another prerequisite for an enhancing effect of stress on memory: stress has to be experienced within the context of the learning episode and vice versa. We presented participants stress context-related words and found memory for these words similarly impaired as memory for stressor-unrelated words. However, were the stressor and stressor-related words really experienced as belonging together? When is information part of the stress context? A critical factor could be that the learned material is relevant for coping with stress. In general, there seems to be a consensus that the physiological stress responses are aimed at coping with the demands of the stressful situation (de Kloet, Joels, & Holsboer, 2005; McEwen, 1998). It is therefore reasonable to assume that stress responses focus our attention primarily to stimuli or information that either cause stress or might help to master the stressful situation. If contextual convergence between stress and learning episode means that the learned information has to be of relevance for coping with stress, then words (whether conceptually related or unrelated to the stressor) were most likely not associated with the stressor; nor was stress an intrinsic part of the learning episode. This may explain why memory for words was impaired in the present study whereas, for example, the memory for the escape platform location was enhanced in rats that were trained in a stressful low temperature version of the Morris water maze (Sandi et al., 1997). Based on these considerations, we suggest an extension of the model by Joels et al. (2006). Learning under stress enhances memory for material that is relevant for coping with the current stressful situation (and similar future situations); a mere contextual relatedness appears to be not sufficient. Furthermore, stress might impair memory even when it occurs around the time of learning, namely when the information is irrelevant for coping with the stressor. To date, it is not clear whether these assumptions apply solely for learning under stress or also for learning shortly before or after stress. Recent evidence suggests that a conceptual relatedness of stress and the learned information might lead to enhanced memory when participants learn briefly after stress (Smeets et al., 2009). Learning after stress differs, however, critically from learning under stress in that after the stress situation is over attention is most likely less focused to the stressor and its properties.

Stress had most likely a significant impact on participants' attentional state during encoding. It appears reasonable to assume that stressed participants, who were emotionally more aroused than controls and had to look into the video camera, could not attend equally to the presented words as controls. The stressor may be seen as a secondary task resulting in a divided attention condition for participants in the stress group. Divided attention at encoding is well known to have adverse effects on subsequent memory performance (e.g. Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000; Foerde, Knowlton, & Poldrack, 2006; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Naveh-Benjamin, Guez, & Marom, 2003). For example, participants that were presented a visual distractor task while simultaneously encoding an auditory word list were significantly impaired in their later memory for the words (Craik et al., 1996; Fernandes & Moscovitch, 2000). A similar impairment was found when participants learned words while performing an auditory trace-discrimination task (Iidaka et al., 2000). These findings parallel those of the present experiment suggesting that stress at encoding that is unrelated to the learning episode may operate as a distractor diverting attention from the learning material.

Effects of stress on initial processing could have been tested by a recall test immediately after learning. Such a test, however, would not have provided an unbiased measure of initial information processing as it would have been affected by stress hormones that remain elevated for a relatively long time after stress. Furthermore, reactivating the memory shortly after the stress exposure might have changed the memory representation (Cai, Blundell, Han, Greene, & Powell, 2006; Schwabe, Bohringer, et al., 2008). Thus, we decided against an immediate recall test.

Besides the assumed effect of divided attention stress might have also caused a general attention deficit. Converging lines of evidence suggest a critical role of the prefrontal cortex in attention processes (Buschman & Miller, 2007; Everling, Tinsley, Gaffan, & Duncan, 2002; Rossi, Pessoa, Desimone, & Ungerleider, 2009). Interestingly, neurotransmitters that are rapidly released in response to stress, such as noradrenaline and dopamine, can disrupt prefrontal cortex structure and function (for a review see Arnsten, 2009). Thus, in addition to the above suggested effect on hippocampal encoding processes an impairing effect of stress on attentional processes mediated by the prefrontal cortex appears possible.

Context-related words were remembered best, both in the stress and in the control group. This is not surprising as words related to the treatment reached most likely deeper levels of processing (Craik & Lockhart, 1972) and remembering the treatment may have facilitated memory for these words at retrieval. It is noteworthy that some of the context-related words (e.g. cold) were related to the stress condition but not to the control condition. Nevertheless, stressed participants' memory was even for context-related words impaired relative to the memory of control participants which underlines the disruptive effect of learning under stress on subsequent memory.

Information that is emotionally arousing is usually very well remembered (Buchanan, 2007; Phelps, 2006; Wolf, in press). In line with the literature, participants remembered in the present study more emotional than neutral words. A dramatic example of the superior memory for emotionally arousing material is the memory for traumatic events like a car accident, warfare or the death of a beloved person. Learning under such extreme stress leads in some people to the development of a posttraumatic stress disorder (PTSD; Olff, Langeland, & Gersons, 2005) in which the strong memory for the traumatic event is a key characteristic. Importantly, in traumatic experiences, stress is an intrinsic part of the experience and supports therefore, unlike in the present study, memory formation.

Although stress had no differential effect on memory in men and women, women remembered overall more words than men. Sex differences in cognition have been repeatedly reported (Cahill, 2006) and there is evidence that women perform better in memory tests than men (Buchanan & Tranel, 2008; Kimura & Clarke, 2002; Kimura & Seal, 2003). Nevertheless, we think the sex difference obtained in the present study should not be overemphasized as it was found in the recall test only; recognition performance was comparable in men and women. Furthermore, we tested two times more women than men which makes a thorough analysis of sex differences difficult. Another limitation of the present experiment is that we presented only neutral words that were related to the stress context. This was because there was not enough time during the

SECPT to present in addition to the 32 words also an appropriate number of positive and negative stress-related words. There is some first evidence that the emotional arousal of context-related information is important for the effect shortly after learning (Smeets et al., 2009). Whether this is also true when people learn under stress has to be assessed in future studies.

In summary, we show that learning under stress, i.e. during the early phase of the stress response, can have detrimental effects on subsequent memory performance. One possible explanation seems to be that stress acted as a distractor during encoding, diverting attention from the learning material. Our findings may have important implications for educational and professional settings. Moreover, they point to necessary extensions of current theories on stress and memory. Unraveling the neural and neuroendocrine mechanisms underlying this effect is a challenge for future research.

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