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Brief Communication

Stress disrupts context-dependent memory

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Memory is facilitated when the retrieval context resembles the learning context. The brain structures underlying contextual influences on memory are susceptible to stress. Whether stress interferes with context-dependent memory is still unknown. We exposed healthy adults to stress or a control procedure before they learned an object-location task in a room scented with vanilla. Memory was tested 24 h later, either in the same or in a different context (unfamiliar room without the odor). Stress administered prior to encoding abolished the context-dependent memory enhancement found in the control group. Thus, these findings represent the first demonstration of impaired context-dependent memory following stress.

Information is better recalled when the retrieval environment resembles the previous learning environment (Tulving and Thompson 1973; Smith and Vela 2001). In a classic example of contextual effects on memory, Godden and Baddeley (1975) asked divers to learn lists of words either on dry land or underwater and tested the memory for these words subsequently either in the same or the opposite environment. Those divers who had to recall the words in the original environment remembered significantly more words than those required to change environments. Recent studies suggest that the hippocampus and the prefrontal cortex are likely candidates for context-dependent memory in the brain (Wagner et al. 1998; Kalisch et al. 2006; Rasch et al. 2007). Interestingly, both of these structures express a high density of receptors for glucocorticoids (cortisol in humans), the steroid hormones that are released from the adrenal cortex in response to stress, and are highly sensitive to stress (de Kloet et al. 2005; Wolf 2008). Memory functions that rely on the integrity of the hippocampus or prefrontal cortex, such as spatial or working memory, are often impaired when stress or cortisol was administered before learning (Lupien et al. 1999; Schwabe et al. 2007; Schoofs et al. 2008; but see also Nater et al. 2007 and Schwabe et al. 2008a for reports of enhanced memory following prelearning stress). Moreover, stress and cortisol suppress memory-related neuroplasticity processes, such as long-term potentiation, in both the hippocampus and the prefrontal cortex (Diamond et al. 2007). In the same line, rodent studies argue that stress before training impairs spatial memory due to a stress-induced suppression of hippocampal spine plasticity (Diamond et al. 1999, 2006). Thus, it could be predicted that stress impairs the beneficial effect of congruent learning and retrieval environments on memory performance. This prediction, however, has not been tested yet.

In the present study, we examined the influence of stress on context-dependent memory in 72 young adults (36 women; age 18–35 yr, $M \pm SEM$: 25.0 ± 0.5 yr). Participation was restricted to healthy nonsmokers. Women that used oral contraceptives (OCs) were excluded because OCs change the cortisol stress response (Kirschbaum et al. 1999). Participants were asked to refrain from meals, drinking alcohol or caffeine, and severe physical exercise within the 2 h before the experiment. All subjects provided written informed consent for their participation in the protocol as approved by the ethics committee of the German Psychological Society (DGPs). Participants were exposed to a stress or control

procedure before they learned an object location task in a room scented with a vanilla odor. On the following day, retention performance was tested either in the same room where learning had taken place and again with the vanilla odor present (congruent context) or in a different room without the odor (incongruent context), resulting in four experimental conditions (9 men and 9 women per condition): stress/congruent context, stress/incongruent context, control/congruent context, and control/incongruent context.

In the stress condition, participants were exposed to the socially evaluated cold pressor test (SECPT) as described elsewhere (Schwabe et al. 2008b). Briefly, participants immersed their hand up to and including the wrist for up to 3 min (or until they could no longer tolerate it) in ice water (0°C – 2°C). They were monitored by an unfamiliar person and videotaped during hand immersion as social evaluation is critical for stress induction (Dickerson and Kemeny 2004). Participants in the control condition submerged their hand up to and including the wrist for 3 min in warm water (35°C – 37°C); they were neither monitored nor videotaped. To assess the efficacy of the SECPT, saliva samples were collected by means of Salivette (Sarstedt) collection devices immediately before as well as 1 min, 20 min, and 35 min after cessation of the SECPT or control condition. Free cortisol concentrations were measured from saliva using an immunoassay (IBL). Moreover, blood pressure measurements were taken immediately before, during, and immediately after the SECPT or control condition, and subjects rated immediately after the SECPT or control condition on a scale from 0 (“not at all”) to 100 (“very much”) how stressful, painful, and unpleasant they had experienced the previous situation.

Twenty-five minutes after the SECPT or control condition, participants went to another room where they were presented with a computer version of the well-known card game “memory” (also known as “concentration”). This interval between stress and learning had been chosen because cortisol reaches peak levels at about 20–30 min after stress (Schoofs et al. 2008; Schwabe et al. 2008b). Subjects saw a configuration of 15 card pairs (5 pictures \times 6 rows) showing colored pictures. First, all cards were shown as gray squares (“laid face down”). Next, participants could choose two cards and turn them face up. If the two cards showed the same picture, subjects could turn the next two cards. If they were not the same, the second card was turned face down again and subjects had to continue their search for the matching card.

Participants were requested to turn over all pairs of matching picture cards as fast as possible. Pictures were taken from the International Affective Picture System (Lang et al. 1997) and varied in emotional valence from neutral to positive and negative.

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Negative pictures (arousal ratings taken from Lang et al. [1997], $M \pm SEM$: 6.8 ± 0.3) were associated with significantly higher emotional arousal than positive pictures (4.5 ± 0.1), which were more arousing than neutral pictures (2.9 ± 0.1 ; $P < 0.001$). Participants completed four trials of the memory task. They were asked to memorize the picture locations as these would be tested later. The spatial arrangement of the cards was randomized across subjects but constant for each subject. During learning we presented a vanilla odor as earlier studies showed that odors are very potent context cues facilitating memory (Rasch et al. 2007).

Twenty-four hours later, participants returned to the laboratory and completed one further trial of the memory task. Importantly, retention testing took place either in the same, *congruent* context (same room and same odor) or in a different, *incongruent* context (new room in a different part of the university building without the odor). Memory performance was expressed as (1) the number of hits (correct card-pair locations without error) in the test trial on day 2 relative to the number of hits in the last training trial on the previous day and (2) the time needed to complete the memory game on day 2, minus the time needed to complete the memory game in the last training trial 24 h before. All testing took place between 1:00 p.m. and 5:30 p.m. to control for the diurnal rhythm of cortisol (Kirschbaum and Hellhammer 1994).

Significant increases in salivary cortisol (stress \times time points of measurement interaction: $F_{(3,189)} = 21.23$, $P < 0.001$; see Fig. 1), systolic and diastolic blood pressure (both $F_{(2,128)} > 30$, both $P < 0.001$; see Table 1) as well as the subjective ratings of stressfulness, painfulness, and unpleasantness (all $F_{(1,64)} > 120$, $P < 0.001$; see Table 1) indicated the success of the stress induction by the SECPT. The physiological and subjective stress responses were comparable in the congruent and incongruent context groups and not influenced by participants' sex (all $P > 0.15$). All subjects except four women and two men (mean duration: 70 sec) underwent the SECPT for the full 3 min. The subjective ratings, blood pressure, and cortisol levels of these 6 participants were, however, not significantly different from the other subjects in the stress group.

All participants improved over the four learning trials (for both hits and time to complete the task both $F_{(3,198)} > 80$, both $P < 0.001$); irrespective of sex, stress, and context condition (all $P > 0.12$). On average, participants scored 11 hits (SEM: 0.3) and

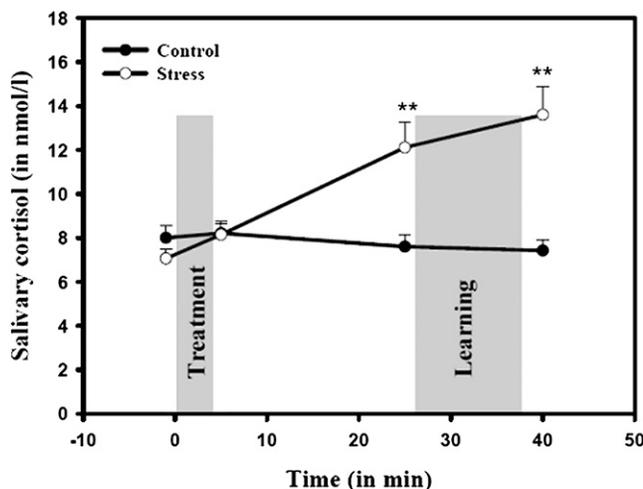


Figure 1. Salivary cortisol concentrations immediately before as well as 1, 20, and 35 min after the socially evaluated cold pressor test (SECPT) or control condition. The gray bars denote the timing and duration of the treatment (SECPT vs. control condition) and the learning phase, respectively. Error bars indicate standard errors of the means. ****** $P < 0.01$.

Table 1. Participants' ratings of stressfulness, painfulness, and unpleasantness, as well as systolic and diastolic blood pressure responses indicated the success of the stress manipulation

	Stress		Control	
	M	SEM	M	SEM
Subjective assessment				
Unpleasant	67.57	4.62	1.67	1.02
Stressful	51.35	4.95	3.33	1.05
Painful	70.00	4.50	0.56	0.39
Systolic blood pressure				
Pre	116.62	2.45	119.83	2.64
During	133.14^a	3.62	114.31	3.82
Post	112.25	2.29	113.05	2.26
Diastolic blood pressure				
Pre	65.55	1.43	67.08	1.38
During	81.19^a	2.13	65.55	1.15
Post	64.83	1.31	65.00	1.17

Boldface: significantly higher in the stress than in the control group ($P < 0.001$).

^aSignificant difference within the stress group ($P < 0.01$).

needed 50 sec for task completion (SEM: 2.5 sec) in the last learning trial. Performance for neutral, positive, and negative pictures was comparable in the final learning trial (between 70% and 75%; $F_{(2,128)} = 0.93$, $P = 0.40$).

In the retention test 24 h later, participants of the control group showed significantly better memory performance, expressed as percentage of hits, if the retrieval context matched the learning context ($t_{(34)} = 2.53$, $P < 0.02$). This memory enhancing effect of congruent learning and testing contexts disappeared when subjects were stressed before learning ($t_{(34)} = 0.19$, $P = 0.85$; context \times stress interaction: $F_{(1,65)} = 4.34$, $P = 0.04$; see Fig. 2). Interestingly, the effects of stress and context depended significantly on the emotionality of the presented pictures (stress \times context \times picture emotionality interaction: $F_{(2,128)} = 3.80$, $P < 0.03$). Stress abolished the context effect on memory most clearly for neutral pictures ($F_{(1,64)} = 8.85$, $P < 0.01$). A comparable trend was found for positive pictures ($F_{(1,64)} = 2.93$, $P = 0.09$), whereas memory for negative pictures remained virtually unaffected by stress and context ($P > 0.90$; see Fig. 2). The main effects of stress, context, and picture emotionality did not reach statistical significance (all $P > 0.13$).

All participants completed the memory task faster when the learning and retrieval contexts were congruent ($F_{(1,64)} = 7.58$, $P < 0.01$; Δ time for task completion ($M \pm SEM$; in seconds): 13.9 ± 3.1 in congruent vs. 29.3 ± 4.4 in incongruent context), while there were no effects of stress or picture emotionality in the time needed to complete the memory task (all $P > 0.17$). Overall, memory performance was unaffected by participants' sex (all $P > 0.15$).

To summarize, our findings support the hypothesis that stress administered prior to encoding impairs context-dependent memory. Memory performance in the control group was enhanced overall by about 30% when the retrieval context resembled the learning context. This beneficial context effect disappeared when participants were stressed before learning. Importantly, since the stress-induced elevations in cortisol, sympathetic, and subjective arousal were over at the time of retention testing 24 h after learning, the observed effect is most likely due to stress effects on the integration of context cues in the memory trace rather than on the retrieval of the context. A theoretical context for our findings can be found in Easterbrook's (1959) cue utilization hypothesis, which assumes that increasing levels of emotional arousal result in a restriction of the range of cues that are attended to. In our study, stressed subjects might have focused primarily on

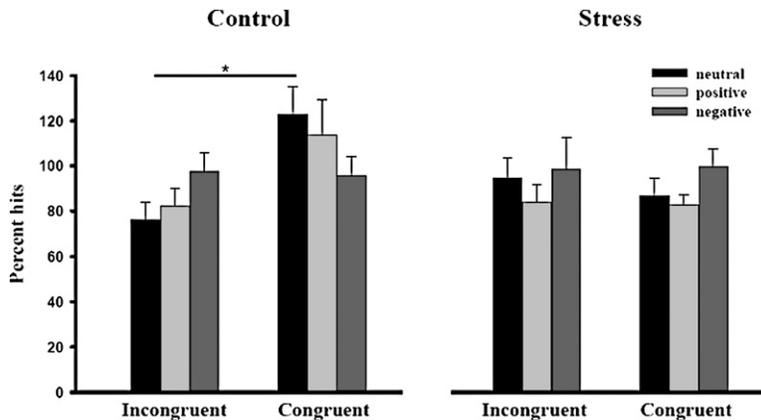


Figure 2. Percent of hits (correct card-pair locations) in the retention test on day 2 relative to the number of hits in the last training trial 24 h before as a function of stress (socially evaluated cold pressor test vs. control condition) and context condition (incongruent vs. congruent context). Note that this measure can yield values >100% if more card-pair locations are recalled in the retention test than in the last training trial. Error bars indicate standard errors of the means. * $P < 0.05$.

information related to the memory task and less to context cues. This interpretation fits well to recent studies showing that stress modulates multiple memory systems in favor of rather simple, caudate nucleus-dependent stimulus–response learning and at the expense of hippocampus-dependent “cognitive” learning which requires the integration of multiple cues (Kim et al. 2001; Schwabe et al. 2007).

Specific learning episodes are automatically embedded within a temporal, spatial, and sensorimotor context. This integration of contextual information into the memory trace is known to rely on the hippocampus (Moscovitch et al. 2005). Thus, our findings suggest that participants stressed before learning do not benefit from the contextual cues when tested for their memory one day later because of reduced hippocampal functioning. This interpretation is in line with electrophysiological evidence showing a reduced neuronal plasticity 20–30 min after stress exposure (Joels et al. 2006; Diamond et al. 2007). It is also in agreement with human fMRI evidence of reduced hippocampal activity following stress (Pruessner et al. 2008) or pharmacological administration of the stress hormone cortisol (Oei et al. 2007).

Importantly, while stress disrupted the context-dependent memory enhancement, the memory for the object-location task per se, which is thought to rely on medial temporal lobe (MTL) structures, was not affected by stress. At first glance, this might appear to be in conflict with previous reports suggesting that stress prior to learning influences MTL-based memory performance. However, the literature on the effects of prelearning stress is very heterogeneous with some studies showing impairing effects (Kirschbaum et al. 1996; Lupien et al. 1997), while others found enhancing effects (Nater et al. 2007; Schwabe et al. 2008a) or no effects at all (Domes et al. 2002). Moreover, these studies tested participants in the same context where learning had taken place, thus, they did not take the influence of the learning/testing environment into account. The fact that stress impaired the use of the context as a cue for memory, whereas memory per se remained unaffected by stress, suggests that both functions rely on medial temporal lobe structures differing in their sensitivity to stress.

Interestingly, the effects of context and stress on memory depended on the valence and arousal of the presented pictures. Context effects were strongest for low arousal (neutral) and weakest for high arousal (negative) pictures. Usually, memory is better for high arousal than for low arousal stimuli (Payne et al. 2006; Buchanan and Tranel 2008; Schwabe et al. 2008a). In line with this view, memory tended to be better for negative than for

positive and neutral pictures in the incongruent context/control condition. Surprisingly, the congruency between learning and retrieval contexts made memory for low arousing pictures not only similar to but even better than memory for high arousing pictures. A possible explanation for this could be the fact that the processing of high arousing information relies on different brain structures than the processing of low arousing information (e.g., amygdalar-hippocampal vs. prefrontal cortex-hippocampal networks [LaBar and Phelps 2002; Kensinger and Corkin 2004]). These structures make memories more stable on the one hand but prevent beneficial influences, e.g., of context congruency, on the other hand.

While stress disrupted the context effect for memory expressed as correctly recalled card-pair locations (hits), the context effect for the time needed to complete the memory task remained unaffected by stress. Similar to other authors who used the same object-location task (Rasch et al. 2007; Benedict et al. 2008), we suggest that accuracy parameters are more sensitive to the influence of memory modulators, such as stress, than speed parameters.

In the present study, the learning context was made up of an odor and a spatial environment. It is important to note that we did not aim to separate the contributions of these context components, but to create a distinct context that may support memory. Nevertheless, previous research suggested that both the memory for odors and the memory for spatial arrangements rely on the hippocampus and adjacent cortices (O’Keefe and Nadel 1978; Burgess et al. 2002; Fortin et al. 2004; Levy et al. 2004). Thus, it is tempting to speculate that there is a common mechanism underlying the impact of stress on odor context-dependent and spatial context-dependent memory enhancement, namely the effect of stress (hormones) on the integrative function of the hippocampus.

Finally, our findings could also be interpreted in light of studies on mood- or state-dependent memory (Lewis and Critchley 2003). According to this view, the presence or absence of stress could be construed as an internal, biological context. As no stress was induced on the test day, this internal context was different for the stress group resulting in incongruent learning and testing contexts in stressed participants tested in congruent spatial and odor environments. Though this interpretation cannot fully account for our findings, future studies are required to include subjects that are re-exposed to stress before retrieval testing to dissect the potential interactions between internal and external context elements.

To conclude, our results suggest that stress can interfere with our ability to integrate context information into a memory trace. These findings might improve our understanding of the pathogenesis of psychiatric disorders, such as the post-traumatic stress disorder in which the failure to connect the traumatic event with the appropriate (temporal and spatial) contextual information is a common pathological hallmark (Rauch et al. 2006).

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