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Research Article

No Retrieval-Induced Forgetting Under Stress

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ABSTRACT—*Stress affects memory, yet no study has investigated the effects of stress on memory inhibition: Remembering not only facilitates later recall, but also inhibits retrieval of related material, a phenomenon known as retrieval-induced forgetting. We investigated the effects of stress on this mechanism, which is thought to adaptively guide memory selection. Participants learned categorized lists and were then exposed to either a psychosocial laboratory stressor or a cognitively challenging control treatment. They then actively retrieved parts of the previously learned material. Finally, memory for all initially learned items was tested. In the stress group, unlike in the control group, intervening retrieval practice did not impair final recall. Moreover, salivary cortisol levels increased and psychological well-being decreased in the stress group only. Thus, psychosocial stress abolishes retrieval-induced forgetting. This effect may result from stress-induced hormone release from the hypothalamic-pituitary-adrenal (HPA) axis and may have implications for educational, legal, and clinical issues.*

Research on the effects of stress on episodic memory has developed into a burgeoning field (for reviews, see, e.g., Joels, Pu, Wiegert, Oitzl, & Krugers, 2006; McGaugh, 2004), and an overall pattern has emerged: In general, acute stress aids memory consolidation (McGaugh & Roozendaal, 2002) and, at least for long-term memory contents, impairs memory retrieval (de Quervain, Roozendaal, & McGaugh, 1998). Glucocorticoid and adrenaline release are assumed to be responsible for these effects. Research on stress in humans typically focuses on the glucocorticoid-releasing hypothalamic-pituitary-adrenal (HPA) axis, and an increase of salivary cortisol levels is often used as a biological marker of activity of the HPA axis during the experience of psychological stress.

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Despite the growing interest in the effects of stress on episodic memory, so far no studies have examined how stress affects retrieval control processes. To be able to focus on currently relevant items and select them from the vast amount of material stored in memory, episodic memory needs efficient retrieval control processes, because, as James (1890) observed,

> If we remembered everything, we should on most occasions be as ill off as if we remembered nothing. It would take as long for us to recall a space of time as it took the original time to elapse, and we should never get ahead with our thinking. (p. 680)

In order to allow for focused retrieval of some memories, other memories need to be at least temporarily inhibited to reduce interference. Indeed, over the past decade, it has been clearly established that remembering itself affects the subsequent availability of related memories. Experimentally, this can be demonstrated with the *retrieval-induced forgetting* paradigm (Anderson, Bjork, & Bjork, 1994). In this paradigm, participants first study a series of category-exemplar pairs (e.g., *fruit-strawberry*, *spice-ginger*, *fruit-apricot*) and then, during retrieval practice, generate half of the exemplars from some of the categories via word-stem completion (e.g., *fruit-ap*_____). This procedure results in three different item types: Rp+ items are the retrieval-practiced items (e.g., *fruit-apricot*), Rp− items are the remaining nonpracticed items from practiced categories (e.g., *fruit-strawberry*), and Nrp items are the nonpracticed exemplars from nonpracticed categories (e.g., *spice-ginger*). The Nrp items serve as control items. Anderson et al. demonstrated that retrieving Rp+ items, not surprisingly, increases their later recall (relative to Nrp items) on a final test. Remarkably, the retrieval practice also reduces the availability of Rp− items, even compared with Nrp items. This phenomenon is referred to as retrieval-induced forgetting.

The effect has been demonstrated to be retrieval specific; that is, it depends on the act of remembering itself: Repeated learning

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of parts of the material is insufficient to cause subsequent forgetting (Anderson, Bjork, & Bjork, 2000; Bäuml, 2002), but retrieval effort alone, regardless of its success, can cause retrieval-induced forgetting (Storm, Bjork, Bjork, & Nestojko, 2006). Furthermore, retrieval-induced forgetting has been demonstrated to be cue independent: It persists even when memory of target items is cued with cues other than the ones initially used. The combined evidence implies that the effect cannot be entirely accounted for by blocking or associative interference, but involves active inhibition (for evidence and discussion, see, e.g., Anderson & Spellman, 1995, or MacLeod & Saunders, 2005, 2008), although from these studies no firm conclusions about the neural basis of the inhibition can be drawn.

The retrieval-induced forgetting effect has been replicated with various modifications of the paradigm (e.g., Ciranni & Shimamura, 1999; MacLeod & Macrae, 2001), and experimental results suggest real-life implications. Retrieval-induced forgetting has been demonstrated in studies on eyewitness memory (Saunders & MacLeod, 2002; Shaw, Bjork, & Handal, 1995), and research has also shown that retrieval-induced forgetting renders memories more susceptible to the misinformation effect: MacLeod and Saunders (2008) demonstrated that memories of items that had been inhibited by previous retrieval-induced forgetting (Rp− items) were later much more affected by misinformation than memories of control (Nrp) or retrieval-practiced (Rp+) items. Interrogators should therefore take great care not to induce retrieval-induced forgetting through repeated selective and suggestive interrogations. The literature on retrieval-induced forgetting also cautions students to be aware of the possibility that practicing only parts of their assignments might reduce the availability of nonpracticed parts more than not practicing at all (Macrae & MacLeod, 1999).

However, so far no study has examined the impact of stress on the mechanisms of retrieval-induced forgetting. More than likely, events such as police interrogations and studying for an exam induce a certain, sometimes even a considerable, level of stress. Stress in turn has been shown to alter episodic memory. Clinically stressed populations, such as patients with acute (Hopwood & Bryant, 2006) or posttraumatic (Bremner, 2006) stress disorder, seem to have almost automatic, easily triggered retrieval of stressful memories. Perhaps for these patients retrieval of some aspects of an episode does not inhibit retrieval of other aspects of the episode, despite the fact that many of these patients have general memory impairments (e.g., Bremner, 2006).

Physiologically, the hippocampus and the prefrontal cortex are involved in retrieval-induced forgetting (Kuhl, Dudukovic, Kahn, & Wagner, 2007), and medial temporal lobe lesions abolish retrieval-induced forgetting (Conway & Fthenaki, 2003). Both the hippocampus and the prefrontal cortex are densely populated with glucocorticoid receptors (e.g., McEwen, De Kloet, & Rostene, 1986; Webster, Knable, O'Grady, Orthmann, & Weickert, 2002), and high cortisol levels impair both hippocampal and prefrontal cortex functioning (Diamond, Campbell, Park, Halonen, & Zoladz, 2007). These considerations suggest that stress may impair retrieval-induced forgetting.

Thus, the experimental question arises whether and how the experience of stress during retrieval of some memories affects the later retrieval of related memories. We addressed this issue by conducting a retrieval-induced forgetting experiment in which stress was induced after learning but before retrieval practice. Participants first learned lists of categorized items. They were then assigned to two groups, one of which was exposed to a psychosocial stressor, the Trier Social Stress Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993; Kudielka, Hellhammer, & Kirschbaum, 2007). The other group was assigned to a cognitive task. The experience of stress was validated via self-report questionnaires and saliva samples measuring cortisol secretion. Immediately after the stress induction, participants had to retrieve some of the previously studied material. In a final recall test, the effect of retrieval practice on the recall of categorically related material was assessed to investigate whether and how acute stress affects retrieval-induced forgetting. To assess the relationship between HPA-axis activity and retrieval-induced forgetting, we calculated the correlation between increase in saliva cortisol and the magnitude of retrieval-induced forgetting.

METHOD

Participants

Forty-eight healthy native German participants (22 females, 26 males) from the University of Konstanz (mean age = 24.71 years, $SE = 0.42$) participated in this study. According to self-reports, all participants were free from acute or chronic diseases. Screening with the German version of the Beck Depression Inventory (BDI; Hautzinger, Bailer, Worall, & Keller, 1994) did not reveal clinically relevant scores in any of the participants (mean BDI score = 5.58, $SE = 0.58$). Participants were asked about a number of variables known to affect the physiological stress response, such as smoking, alcohol consumption, and body weight, and female participants were also asked about their use of oral contraceptives. All subjects were instructed not to eat, drink caloric beverages or caffeine, or smoke for 1 hr before the beginning of the experiment.

In a between-subjects design, participants were randomly assigned to either the stress condition ($n = 24$; 11 women, 13 men) or the control condition ($n = 24$; 11 women, 13 men). The stress and control groups did not differ in age, $F(1, 46) = 0.01$, $p > .90$; body mass index, $F(1, 46) = 0.20$, $p > .60$; smoking habits (7 smokers per group; mean number of cigarettes per week = 17.84, $SE = 5.45$), $F(1, 46) = 1.57$, $p > .20$; or BDI scores, $F(1, 46) = 1.53$, $p > .20$. A Pearson chi-square exact test indicated no group difference in the distribution of use of oral contraceptives, $\chi^2(1, N = 22) = 0.79$, $p > .30$.

The study was approved by the local ethics committee. Subjects provided written informed consent and were given a small

financial compensation for completing the experiment. After the experiment, they were extensively debriefed about the true nature of the study.

Procedure

Each participant was tested in a single session, conducted in the afternoon between 2:00 and 6:00 p.m., when cortisol levels are low. Each session was run either by an individual experimenter (control group) or by a team of three, one experimenter and two members of the "stress induction committee" (see the next paragraph). The sequence of experimental events is depicted in Figure 1.

Treatment: Stress Induction Versus Control Task

Stress Induction—TSST. The TSST (cf. Kirschbaum et al., 1993; Kudielka et al., 2007), which was used as a stressor between the study and retrieval-practice phases, effectively induces stress and activates the HPA axis (Dickerson & Kemeny, 2004; Kirschbaum et al., 1993). The test consists of a public-speaking task and a mental-arithmetic task in which participants have to calculate aloud in public. For the former, participants are asked to take on the role of a job applicant and to give a speech in front of a selection panel. The members of the panel (one female, one male) are confederates who are instructed to withhold facial and verbal feedback and to communicate with the participant in a neutral manner. Sitting in front of the panel, subjects have 3 min to prepare their talk. Then, in a 5-min speech, they have to convince the panel that they are the perfect applicant. In the subsequent 5-min arithmetic task, participants have to serially subtract 13 from 1,687 (i.e., 1,687 − 13 = 1,674, 1,674 − 13 = 1,661, etc.) as quickly and accurately as possible. They must start over from the beginning if they make an error. During the speech and the arithmetic tasks, participants stand in front of the panel, are videotaped, and speak into a microphone.

Control Tasks. The control tasks were comparable to the tasks in the TSST, to ensure an equal cognitive load, but the stressful social components were omitted. Thus, the interview was replaced by a writing assignment; subjects had to imagine that their friend had applied for a new position and were instructed to write a fictitious script for their friend's interview for that job. They had 3 min to prepare and 5 min to write. Then, participants serially subtracted 13 from 1,687 for 5 min, writing each answer on a separate page in a booklet. Every fifth page displayed the correct number for the most recent calculation, so that participants could detect errors and return to previous pages to make corrections.

Retrieval-Induced Forgetting Paradigm

Materials. Eleven categories, two of which were fillers, were chosen from different published norms (Mannhaupt, 1983; Scheithe & Bäuml, 1995). Each category comprised six exemplars, whose initial letters were unique within their category. All experimental material was presented on a laptop computer (Fujitsu Siemens Amilo M 7400) using Presentation software (Neurobehavioral Systems, Inc., Albany, NY).

Study Phase. Sixty-six category-exemplar pairs (e.g., *fruit-strawberry*, *spice-ginger*, *fruit-apricot*) were presented in a blocked randomized order. Each block consisted of 11 items and contained 1 exemplar from each category. Two items from the same category were never presented consecutively. The first 2 exemplars of the first block and the last 2 exemplars of the last block were from the filler categories. Each category-exemplar pair was shown for 5 s; the interstimulus interval (ISI) was 200 ms.

Retrieval-Practice Phase. In the retrieval-practice phase, which directly followed the stress (or control) treatment, participants practiced half of the exemplars from six of the nine relevant categories. On each trial, a category name and word stem were presented, and participants had to complete the exemplar (e.g., *fruit-ap*_____) aloud. Each category-stem pair was shown for 2.5 s; the ISI was 200 ms. Exemplars from one filler category were included and served to control for primacy and recency effects. Across subjects and conditions, the assignment of categories to retrieval practice (resulting in Rp+ and Rp− items) or no retrieval practice (Nrp items) was counterbalanced. All category-stem pairs were practiced three times. Successive presentation of members of the same category was avoided.

To maintain the stress experience during the retrieval-practice phase, we had participants in the stress condition perform this phase together with the TSST committee, which jotted down participants' answers. Subjects in the control group performed this phase together with the experimenter, who wrote down the responses.

Final Test Phase. For the final test, the previously learned exemplars were presented in a categorized blocked order (2.5 s per item, ISI = 200 ms). On each trial, a category name and initial letter of an exemplar were displayed, and participants had to name the exemplar aloud (e.g., *fruit-a*_____). To acquaint participants with the procedure, we presented items from one of the two filler categories first. The order of the remaining categories was randomized, as was the order of the items within each category, to control for output interference effects. The stress and control groups both performed this part of the experiment with the experimenter, who wrote down the responses.

Manipulation Check

Saliva cortisol concentration was used as a physiological stress marker (e.g., Dickerson & Kemeny, 2004). Saliva samples were obtained with commercial collection devices (Salivette; Sarstedt, Nümbrecht, Germany). Additionally, we used questionnaires to assess relevant clinical variables and psychological stress responses.

For the baseline cortisol measurement prior to the study phase of the retrieval-induced forgetting procedure, participants had to

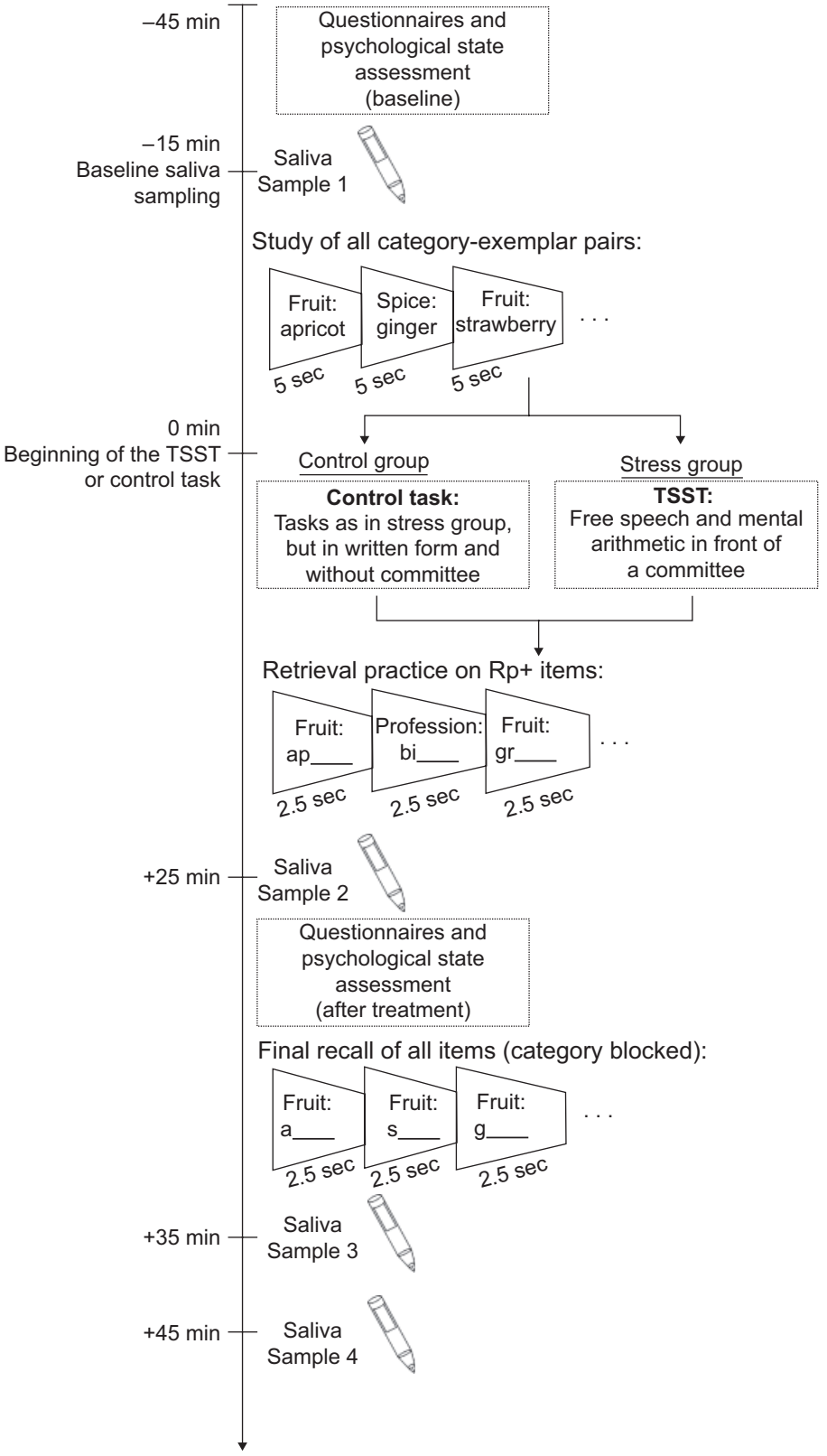

Fig. 1. Experimental procedure. Subjects completed questionnaires and provided a baseline saliva sample, performed the study phase of the retrieval-induced forgetting task, and then completed the treatment, which consisted of the Trier Social Stress Test (TSST) or control tasks with similar cognitive demands but no social stress. Next came the retrieval-practice phase of the retrieval-induced forgetting task, collection of a second saliva sample, the second administration of questionnaires, a final recall test on the studied items, and collection of two final saliva samples.

rest for approximately 30 min (see Fig. 1). They did not yet know the group to which they had been assigned. During this period, participants filled in a German version of the BDI (Hautzinger et al., 1994); the German version of the State–Trait Anxiety Inventory (STAI; Laux, Glanzmann, Schaffner, & Spielberger, 1981); a German psychological state scale, the Befindlichkeits-Skala (Bf-S; von Zerssen & Koeller, 1976); a German stress-coping questionnaire, the Streßverarbeitungsfragebogen (SVF 120; Janke, Erdmann, Kallus, & Boucsein, 1997); and a competence- and control-orientations questionnaire, the Fragebogen zu Kompetenz- und Kontrollüberzeugungen (FKK; Krampen, 1991). The SVF and FKK were not fully completed by all subjects and were not further analyzed. They were used primarily to engage the participants in a controlled manner during the period prior to the baseline saliva sampling.

Fifteen minutes prior to the baseline saliva sampling, all participants drank 300 ml of grape juice to standardize blood glucose levels, as suggested by Kudielka et al. (2007). To measure stress-induced changes in salivary cortisol, we took three additional samples 25, 35, and 45 min after the beginning of the TSST or control task. The STAI and Bf-S were administered a second time after the retrieval-practice phase, just after the second saliva sampling (see Fig. 1). On these measures, participants retrospectively assessed their psychological state during the treatment and the retrieval-practice phase. At this time, we also measured subjects' perception of task (TSST or control task) requirements using seven visual analogue scales. By marking the appropriate point on a line ranging from *not at all* to *extremely*, participants indicated their personal involvement in the task; how new, difficult, stressful, unpredictable, and personally challenging the task was; and whether they anticipated negative consequences from poor performance.

Saliva samples were stored at −20 °C until assayed. Cortisol levels were measured using a competitive bead-based assay. Undiluted saliva or cortisol standard dilutions were incubated overnight in 96-well round-bottom plates with cortisol-BSA (bovine serum albumin)-conjugated polystyrene beads and fluorescein isothiocyanate (FITC)-conjugated rabbit anticortisol antibody (HTB192; Chromaprobe, Maryland Heights, MO). After incubation, beads were washed and resuspended in phosphate-buffered saline, and analyzed on an LSR II flow cytometer equipped with a high-throughput sampler (BD Immunocytometry Systems, San Jose, CA). The median fluorescence intensity measured in this analysis is inversely proportional to the amount of cortisol in the sample.

RESULTS

Manipulation Check: Stress Induction Versus Control Task

Cortisol Levels

As expected, stressed subjects showed a significant increase in salivary cortisol after the TSST. A repeated measures analysis of variance (ANOVA) with the factors of treatment (stress or control) and measurement time (baseline or 25, 35, or 45 min after onset of the treatment) yielded a significant treatment-by-time interaction, $F(3, 138) = 13.44, p < .001$. Post hoc t tests showed that stressed and control participants' cortisol levels differed significantly 25 min after treatment onset, $t(46) = 3.27$, $p < .01$; 35 min after treatment onset, $t(46) = 3.57$, $p < .001$; and 45 min after treatment onset, $t(46) = 3.91$, $p < .001$; baseline levels were comparable in the two groups, $t(46) = -1.19$, $p > .20$. Figure 2 depicts the time course of cortisol levels in the two groups.

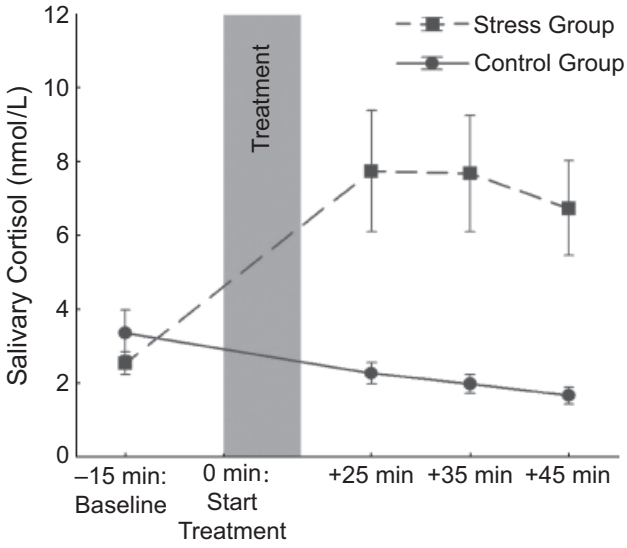

Fig. 2. Mean cortisol levels of the stress and control groups as a function of time. Error bars represent standard errors.

Psychological Assessment

STAI. A repeated measures ANOVA with the factors of measurement time (before or after treatment) and treatment (stress or control) revealed that state anxiety was significantly increased after the TSST, $F(1, 46) = 7.40$, $p < .01$, although baseline state anxiety did not differ between the TSST and control groups, $t(46) = 1.17$, $p > .20$.

Bf-S. Likewise, the Bf-S yielded a significant Treatment × Measurement Time interaction, $F(1, 46) = 4.76$, $p < .05$. The psychological state of the stressed participants had significantly deteriorated after the TSST, whereas no such effect occurred in the control participants. Psychological state at baseline did not differ between the two groups, $t(46) = 0.54$, $p > .50$.

Visual Analogue Scales. The analysis of the seven visual analogue scales revealed that subjects rated the TSST as significantly more difficult, $F(1, 46) = 24.39, p < .001$; more stressful, $F(1, 46) = 20.50, p < .001$; and more unpredictable, $F(1, 46) = 13.76, p < .001$, than the control treatment. The subjects' ratings of the stress and control treatments did not differ in terms of personal challenge, $F(1, 46) = 3.30$, $p > .05$; anticipation of

negative consequences, $F(1, 46) < 1$; personal involvement, $F(1, 46) < 1$; or novelty, $F(1, 46) = 1.63$, $p > .20$.

Memory Performance

Retrieval Practice

Control subjects retrieved 77.31% ($SE = 2.17\%$) of the items during the retrieval-practice phase. Stressed subjects remembered 78.55% ($SE = 2.43\%$) of the items. The groups did not differ significantly in retrieval-practice performance, $F(1, 46) < 1$.

Final Recall Test

Practice Effect. To examine whether the psychosocial stress experience affected the practice effect (i.e., whether previously practiced words were recalled better than control words), we conducted an ANOVA with word type (Rp+, Nrp) as a repeated measures factor and treatment (stress, control) as a between-groups factor. Results showed that subjects in both groups exhibited a clear training effect, $F(1, 46) = 74.17$, $p < .001$. Neither the main effect of treatment nor the Treatment × Word Type interaction was significant, Fs$(1, 46) < 1$ (see Fig. 3).

Retrieval-Induced Forgetting. We conducted a 2 (treatment: stress, control) × 2 (word type: Rp−, Nrp) repeated measures ANOVA to investigate whether stress affected the retrieval-induced forgetting effect. The analysis yielded a significant Treatment × Word Type interaction, $F(1, 46) = 6.57$, $p = .01$.

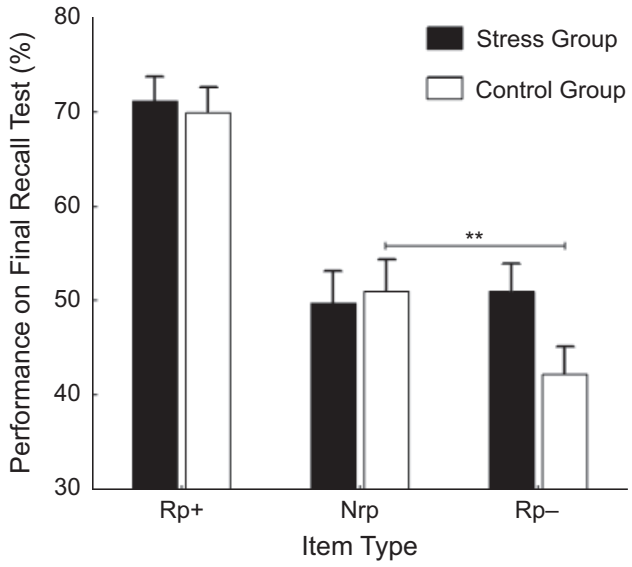

Fig. 3. Percentage of items recalled on the final recall test as a function of condition (stress or control) and item type. The item types are as follows: retrieval-practiced items, Rp+; the remaining nonpracticed items from practiced categories, Rp−; and nonpracticed exemplars from nonpracticed categories, Nrp. A training effect is indicated by better performance on Rp+ items than on Nrp items, and retrieval-induced forgetting is indicated by lower performance on Rp− than on Nrp items. Error bars represent standard errors. The asterisks indicate a significant difference between item types ($p < .01$).

Post hoc analyses with paired t tests showed that performance on Rp− items was reduced relative to performance on Nrp items only in the control group, $t(23) = 3.37$, $p < .01$; no performance difference was found in the stress group, $t(23) = 0.14$, $p > .60$. Thus, retrieval-induced forgetting occurred in the control group, but not in the stress group. The main effect of treatment was not significant, $F(1, 46) < 1$. The main effect of word type was marginally significant, $F(1, 46) = 3.87$, $p = .06$. Memory performance for the different item types is depicted in Figure 3.

Correlation Between Cortisol Level and Retrieval-Induced Forgetting

We calculated a correlation to assess the relationship between the degree of retrieval-induced forgetting and individual cortisol level. For this analysis, our measure of retrieval-induced forgetting was calculated from the percentages of correct answers as follows: [Nrp − (Rp−)]/Nrp (cf. Kuhl et al., 2007). The Spearman rank correlation between the magnitude of retrieval-induced forgetting and the maximum cortisol increase compared with the baseline level was significant ($r_s = -.29$, $N = 48$, $p < .05$).

DISCUSSION

This research investigated the effect of psychosocial stress on retrieval-induced forgetting, an inhibitory retrieval control mechanism thought to aid selection of relevant memory contents from episodic memory. The study extends knowledge about the effects of stress on episodic memory, showing that these effects are not limited to consolidation and retrieval, but are also found for retrieval inhibition. The typical retrieval-induced forgetting effect (i.e., reduced recall of nonpracticed items after retrieval of related material) was absent after exposure to a psychological stressor whose effectiveness was demonstrated by an increase in HPA activity (as reflected by a rise in salivary cortisol secretion), an increase in state anxiety, and a decrease on a measure of psychological well-being.

Although the experience of stress shortly before retrieval impairs recall performance for well-consolidated memories (de Quervain et al., 1998; Kuhlmann, Piel, & Wolf, 2005), no such impairment was observed in the present study. Instead, the typically reported retrieval-induced memory impairment, which was observed in the control group, was absent in the stress group. Perhaps paradoxically, this finding demonstrates that at least relatively shortly after encoding, stress does not necessarily impair retrieval, but, by way of releasing memory contents from retrieval inhibition, can even lead to a relative improvement of memory performance. Retrieval-induced forgetting has previously also been shown to affect well-consolidated episodic (MacLeod & Macrae, 2001) and semantic (Anderson & Bell, 2001) memories, but the present findings leave open the possibility that the elimination of retrieval-induced forgetting by stress might be restricted to relatively recent memories. Alternatively, at longer testing delays, stress might produce both

general retrieval impairment and an elimination of retrieval-induced forgetting.

Previous work provides clues as to cognitive and physiological processes that might mediate stress-induced release from retrieval-induced forgetting. Cognitively, the occurrence of retrieval-induced forgetting depends on the degree of relational processing between the presented items within a category: If no relationship between items is established and all items are processed in isolation, in an item-specific manner, retrieval-induced forgetting disappears, and a recent study has suggested that this is the case when negative mood is induced in participants (Bäuml & Kuhbandner, 2007).

A possible physiological account of the effect of stress on retrieval-induced forgetting derives from work showing that stress impairs the contextual binding of items to episodes (Payne, Nadel, Allen, Thomas, & Jacobs, 2002), an ability supported by the hippocampus (Nadel, Payne, & Jacobs, 2002). Given that medial temporal lobe structures appear critical in retrieval-induced forgetting (Conway & Fthenaki, 2003), the effects observed in the present study may have been due to glucocorticoid-mediated release from episodic binding that, in turn, resulted in item-specific processing.

Retrieval-induced forgetting, although associated with a reduction in the number of items available for recall, is typically viewed as an adaptive mechanism (MacLeod & Saunders, 2008). People who exhibit larger retrieval-induced forgetting effects are in general less forgetful and less prone to everyday cognitive errors (Groome & Grant, 2005), a finding that seems to confirm James's (1890) intuition that memory, to function efficiently, needs selection that renders some contents at least temporarily inaccessible. However, the apparent long-term advantage associated with retrieval-induced forgetting clearly comes at a momentary cost. Under stress, this cost disappears, at least temporarily. In the short run, stress responses are often favorable evolutionary adaptations. Although free recall from long-term memory is impaired under stress, the normally operational retrieval inhibition of items that are episodically or semantically related to already recalled material may be suspended. HPA-axis activity, as reflected in increased salivary cortisol, could mediate this release from retrieval inhibition. Humans may benefit from this effect in exam situations or during legal interrogations. In fact, the present results suggest the perhaps counterintuitive possibility that even susceptibility to misinformation effects may decrease in stressful situations (MacLeod & Saunders, 2008). However, if the stress response persists, this short-term blessing may turn into a long-term burden: the burden of undesired memories experienced by patients with post-traumatic stress disorder.

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REFERENCES

Anderson, M.C., & Bell, T. (2001). Forgetting our facts: The role of inhibitory processes in the loss of propositional knowledge. *Journal of Experimental Psychology*, *130*, 544–570.

Anderson, M.C., Bjork, E.L., & Bjork, R.A. (2000). Retrieval-induced forgetting: Evidence for a recall-specific mechanism. *Psychonomic Bulletin & Review*, *7*, 522–530.

Anderson, M.C., Bjork, R.A., & Bjork, E.L. (1994). Remembering can cause forgetting: Retrieval dynamics in long-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 1063–1087.

Anderson, M.C., & Spellman, B.A. (1995). On the status of inhibitory mechanisms in cognition: Memory retrieval as a model case. *Psychological Review*, *102*, 68–100.

Bäuml, K.-H. (2002). Semantic generation can cause episodic forgetting. *Psychological Science*, *13*, 356–360.

Bäuml, K.-H., & Kuhbandner, C. (2007). Remembering can cause forgetting—but not in negative moods. *Psychological Science*, *18*, 111–115.

Bremner, J.D. (2006). Traumatic stress: Effects on the brain. *Dialogues in Clinical Neuroscience*, *8*, 445–461.

Ciranni, M.A., & Shimamura, A.P. (1999). Retrieval-induced forgetting in episodic memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 1403–1414.

Conway, M.A., & Fthenaki, A. (2003). Disruption of inhibitory control of memory following lesions to the frontal and temporal lobes. *Cortex*, *39*, 667–686.

de Quervain, D.J., Roozendaal, B., & McGaugh, J.L. (1998). Stress and glucocorticoids impair retrieval of long-term spatial memory. *Nature*, *394*, 787–790.

Diamond, D.M., Campbell, A.M., Park, C.R., Halonen, J., & Zoladz, P.R. (2007). The temporal dynamics model of emotional memory processing: A synthesis on the neurobiological basis of stress-induced amnesia, flashbulb and traumatic memories, and the Yerkes-Dodson law. *Neural Plasticity*, *2007*, Article 60803. Retrieved August 2009 from http://www.hindawi.com/journals/np/2007/060803.abs.html

Dickerson, S.S., & Kemeny, M.E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*, 355–391.

Groome, D., & Grant, N. (2005). Retrieval-induced forgetting is inversely related to everyday cognitive failures. *British Journal of Psychology*, *96*, 313–319.

Hautzinger, M., Bailer, M., Worall, H., & Keller, F. (1994). *Beck-Depressions-Inventar (BDI)*. Bern, Germany: Huber.

Hopwood, S., & Bryant, R.A. (2006). Intrusive experiences and hyperarousal in acute stress disorder. *British Journal of Clinical Psychology*, *45*, 137–142.

James, W. (1890). *The principles of psychology* (Vol. 1). New York: Holt.

Janke, W., Erdmann, G., Kallus, K.W., & Boucsein, W. (1997). *Streßverarbeitungsfragebogen (SVF 120)*. Göttingen, Germany: Hogrefe.

Joels, 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.

Kirschbaum, C., Pirke, K.-M., & Hellhammer, D.H. (1993). The 'Trier Social Stress Test'—a tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology*, *28*, 76–81.

Krampen, G. (1991). *Fragebogen zu Kompetenz- und Kontrollüberzeugungen (FKK)*. Göttingen, Germany: Hogrefe.

Kudielka, B.M., Hellhammer, D.H., & Kirschbaum, C. (2007). Ten years of research with the Trier Social Stress Test—revisited. In E. Harmon-Jones & P. Winkielman (Eds.), *Social neuroscience: Integrating biological and psychological explanations of social behavior* (pp. 56–83). New York: Guilford Press.

Kuhl, B.A., Dudukovic, N.M., Kahn, I., & Wagner, A.D. (2007). Decreased demands on cognitive control reveal the neural processing benefits of forgetting. *Nature Neuroscience*, *10*, 908–914.

Kuhlmann, S., Piel, M., & Wolf, O.T. (2005). Impaired memory retrieval after psychosocial stress in healthy young men. *Journal of Neuroscience*, *25*, 2977–2982.

Laux, L., Glanzmann, P., Schaffner, P., & Spielberger, C.D. (1981). *Das State-Trait-Angstinventar, Theoretische Grundlagen und Handanweisungen*. Weinheim, Germany: Beltz.

MacLeod, M.D., & Macrae, C.N. (2001). Gone but not forgotten: The transient nature of retrieval-induced forgetting. *Psychological Science*, *12*, 148–152.

MacLeod, M.D., & Saunders, J. (2005). The role of inhibitory control in the production of misinformation effects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*, 964–979.

MacLeod, M.D., & Saunders, J. (2008). Negative consequences of an adaptive process: Retrieval inhibition and memory distortion. *Current Directions in Psychological Science*, *17*, 26–30.

Macrae, C.N., & MacLeod, M.D. (1999). On recollections lost: When practice makes imperfect. *Journal of Personality and Social Psychology*, *77*, 463–473.

Mannhaupt, H.-R. (1983). Produktionsnormen für verbale Reaktionen zu 40 geläufigen Kategorien. *Sprache & Kognition*, *4*, 264–278.

McEwen, B.S., De Kloet, E.R., & Rostene, W. (1986). Adrenal steroid receptors and actions in the nervous system. *Physiological Review*, *66*, 1121–1188.

McGaugh, J.L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, *27*, 1–28.

McGaugh, J.L., & Roozendaal, B. (2002). Role of adrenal stress hormones in forming lasting memories in the brain. *Current Opinions in Neurobiology*, *12*, 205–210.

Nadel, L., Payne, J.D., & Jacobs, W.J. (2002). The relationship between episodic memory and context: Clues from memory errors made while under stress. *Physiological Research*, *51*(Suppl. 1), S3–S11.

Payne, J.D., Nadel, L., Allen, J.J., Thomas, K.G., & Jacobs, W.J. (2002). The effects of experimentally induced stress on false recognition. *Memory*, *10*, 1–6.

Saunders, J., & MacLeod, M.D. (2002). New evidence on the suggestibility of memory: The role of retrieval-induced forgetting in misinformation effects. *Journal of Experimental Psychology: Applied*, *8*, 127–142.

Scheithe, K., & Bäuml, K.-H. (1995). Deutschsprachige Normen für Vertreter von 48 Kategorien. *Sprache & Kognition*, *14*, 39–43.

Shaw, J.S.I., Bjork, R.A., & Handal, A. (1995). Retrieval-induced forgetting in an eyewitness-memory paradigm. *Psychonomic Bulletin & Review*, *2*, 249–253.

Storm, B.C., Bjork, E.L., Bjork, R.A., & Nestojko, J.F. (2006). Is retrieval success a necessary condition for retrieval-induced forgetting? *Psychonomic Bulletin & Review*, *13*, 1023–1027.

von Zerssen, D., & Koeller, D.-M. (1976). *Die Befindlichkeits-Skala, Manual*. Weinheim, Germany: Beltz.

Webster, M.J., Knable, M.B., O'Grady, J., Orthmann, J., & Weickert, C.S. (2002). Regional specificity of brain glucocorticoid receptor mRNA alterations in subjects with schizophrenia and mood disorders. *Molecular Psychiatry*, *7*, 985–994.

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