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Stress-induced bias of multiple memory systems during retrieval depends on training intensity

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ABSTRACT

Stressful events promote a shift from hippocampus-dependent 'cognitive' learning towards dorsal striatum-dependent 'habit' learning. Beyond modulating the recruitment of multiple memory systems during learning, recent evidence suggests that stress may also affect which of these memory systems is employed during retrieval, thereby affecting the nature of remembering. However, while some studies reported increased reliance on 'habit' memory retrieval after stress, other studies suggested even a bias towards 'cognitive' memory retrieval after stress. In the present experiment, we tested the hypothesis that the nature of the stress effect on the control of memory retrieval depends on the extent of initial training. To this end, participants completed a probabilistic classification learning (PCL) task that can be solved by both the 'cognitive' and the 'habit' memory systems, which is reflected in the engagement of specific behavioral strategies. Critically, participants received either moderate (100 trials) or intensive (200 trials) training in the PCL task. Participants then underwent a stress protocol or a non-stressful control procedure, before they completed a retrieval version of the PCL task. The effectiveness of the stress manipulation was verified by increases in salivary cortisol and autonomic arousal. Our results further revealed that participants who received moderate training showed, during retrieval, a stress-induced shift towards strategies indicative of the dorsal striatal 'habit' memory system. After prolonged training, however, stress did not affect which memory system guided retrieval. The present results indicate that the effect of stress on the engagement of multiple memory systems during retrieval is critically dependent on the extent of initial training and, by inference, on the strength of the multiple memory traces established during learning.

1. Introduction

Stressful events are known to have a critical impact on learning and memory. In particular, research over the past decades has shown that stress can enhance memory formation but impair memory retrieval (de Quervain et al., 1998; Cahill et al., 2003; Diamond et al., 2006; Joels et al., 2011; Schwabe et al., 2012a; Vogel and Schwabe, 2016). Beyond quantitative changes in memory consolidation and retrieval, stress can also influence the contribution of multiple, anatomically and functionally distinct memory systems to behavior. Specifically, stress has been shown to promote the engagement of an efficient but rather rigid 'habit' memory system depending on the dorsal striatum, at the cost of a more flexible, but resource-demanding 'cognitive' memory system depending on the hippocampus (Kim et al., 2001; Schwabe et al., 2007, 2010a; Vanelzakker et al., 2011; Packard and Goodman, 2012; Schwabe and Wolf, 2012; Siller-Pérez et al., 2017; Wirz et al., 2018). This stress-induced modulation of memory system engagement depends, same as stress effects on consolidation and retrieval (Roozendaal et al., 2004, 2006a), on the action of glucocorticoids (Schwabe et al., 2010a, 2013; Vogel et al., 2016, 2017; Siller-Pérez et al., 2017) and noradrenaline (Packard and Wingard, 2004; Wirz et al., 2017).

While initial findings showed a stress-induced modulation of 'cognitive' and 'habit' memory systems during learning, accumulating evidence suggests that stress and stress mediators can also affect which of these multiple memory systems is in control when the memories are later retrieved. More specifically, an early study in rodents showed that a pharmacological increase of noradrenergic stimulation before retrieval promoted a shift from hippocampal to striatal control of memory retrieval (Elliott and Packard, 2008). A recent study from our lab showed a similar stress-related bias towards 'habit' memory retrieval in humans (Zerbes et al., 2020b). There are, however, also findings suggesting that stress and stress mediators may even produce a shift in the

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opposite direction, towards the 'cognitive' memory system (Zerbes et al., 2019, 2020a), thus raising the question how these heterogeneous findings can be reconciled. A potential explanation for the different direction of the stress (hormone) effects on the control of memory retrieval may be the intensity of training. It is well known that the engagement of memory systems during learning changes depending on the extent of training. The 'cognitive' memory system is established rapidly and governs behavior early in learning, while control shifts towards the 'habit' system when learning is more advanced (Poldrack et al., 2001; Gluck et al., 2002; Iaria et al., 2003). However, the 'cognitive' memory established early in training is not damaged in this process, but instead both forms of memory are retained in parallel and can potentially control behavior (Packard and McGaugh, 1996; Chang and Gold, 2003). Interestingly, the studies showing that stress or noradrenergic arousal led to a preference for the 'habit' system during later retrieval used rather moderate training (Elliott and Packard, 2008; Zerbes et al., 2020b), whereas studies that showed a stress-induced bias towards 'cognitive' memory retrieval used extensive training (Zerbes et al., 2019, 2020a). These data suggest that the extent of training may indeed modulate the stress effects on the balance of 'cognitive' and 'habit' memory during retrieval. This hypothesis, however, has not been systematically tested so far.

The present study aimed to elucidate whether the stress-induced bias towards the 'cognitive' or 'habit' memory system during retrieval depends on the extent of practice in the task. To this end, participants first acquired a probabilistic classification learning (PCL) task that can be solved by both the 'cognitive' and the 'habit' memory system (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004b). To investigate the role of the extent of training on the subsequent stress effect on the control of memory retrieval, participants received either moderate (100 trials) or intensive (200 trials) training in the PCL task. Afterwards, participants underwent either a stress protocol or a non-stressful control procedure before they completed a retrieval version of the PCL task. Memory system engagement in the PCL task can be inferred by the utilization of different behavioral strategies (Gluck et al., 2002; Shohamy et al., 2004a; Schwabe and Wolf, 2012). This enabled us to examine the effect of stress on memory system engagement during retrieval and if it depends on the intensity of prior training. Based on previous results (Elliott and Packard, 2008; Zerbes et al., 2019, 2020a, 2020b), we hypothesized that stress after moderate training would induce a bias towards 'habit' memory during retrieval, whereas stress would induce a relapse towards the 'cognitive' memory system, usually recruited early in learning, after prolonged training.

2. Materials and methods

2.1. Participants and experimental design

One-hundred and eleven healthy volunteers participated in this study (53 women, age (mean ± SD): 25.41 ± 3.87). Participants were included if they reported no lifetime history of any mental or neurological disease, no drug- or tobacco-use and no current medication intake. Furthermore, women did not take hormonal contraceptives and were not tested during their menses. All participants provided informed consent before taking part in the study. The study was approved by the local ethics committee of the Universität Hamburg and conducted in accordance with the Declaration of Helsinki.

In a fully-crossed between-subjects design with the factors treatment (stress vs. control) and extent of training (moderate vs. intensive), participants were randomly assigned to one of four experimental groups: stress/moderate training (STRESS/MOD, N = 27), stress/intensive training (STRESS/INT, N = 24), control/moderate training (CON/MOD, N = 35) and control/intensive training (CON/INT, N = 25).

2.2. Experimental tasks and procedure

All testing took place between 13:00 and 18:00 to control for the diurnal rhythm of cortisol. After arriving at the lab, participants filled out a mood questionnaire (German Version of the Positive and Negative Affect Schedule, PANAS, Krohne et al., 1996), provided a saliva sample using a salivette (Sarstedt, Nümbrecht, Germany) collection device. In addition, baseline measurements of blood pressure and pulse were taken using a Critikon Dinamap system (Tampa, FL, USA).

Afterwards, participants completed a PCL task, commonly known as the 'Weather Prediction Task' (Fig. 1, Knowlton et al., 1994, 1996). This task can be solved by both the hippocampal 'cognitive' memory system and the dorsal striatal 'habit' memory system (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004a). Each trial started with the presentation of one, two or three (out of four possible) cue cards. The participant was asked to predict the weather outcome (sun vs. rain) based on the card cues via button press. Following the participant's response, feedback about the correct weather outcome was presented, enabling the participant to learn the associations between the card cues and the weather outcome on a trial-by-trial basis. There were 14 possible card patterns, which were probabilistically linked to the two weather outcomes. These probabilities were determined in a way that the different cards were associated with the outcome 'sun' with a probability of 75.6, 57.5, 42.5 or 24.4% across the task. Responses corresponding to the most probable weather outcome were counted as correct, irrespective of the actual feedback that the participant received. Critically, in order to experimentally manipulate the extent of practice, participants completed either 100 (moderate training) or 200 trials (intensive training) during the learning phase of the PCL task, depending on the experimental group.

After the learning phase, additional measures of blood pressure and pulse were taken, a saliva sample was collected and subjective mood was assessed. Next, participants completed either the Trier Social Stress Test (TSST, Kirschbaum et al., 1993) or a non-stressful control procedure, depending on experimental group assignment. The TSST is a standardized stress-induction paradigm that reliably elicits responses of the hypothalamus-pituitary-adrenal axis and the autonomic nervous system (Kudielka et al., 2007). In brief, the TSST represents a simulated job interview in which participants were asked to give a five-minute free speech, after a preparation time of three minutes. Thereafter, participants had to complete a difficult arithmetic task (counting backwards from 2043 in steps of 17). During both tasks, participants were video-taped and monitored by a cold, non-responsive interview panel consisting of a man and a woman, both dressed in white lab coats. In the control condition, participants gave a five-minute free speech on a topic of their choice, followed by an easy arithmetic task (counting forwards from 0 in steps of 15). During both tasks, participants were alone in a room and were neither monitored nor videotaped. Between the two tasks of the TSST/control manipulation, blood pressure and pulse measurements were taken. After the manipulation, participants rated on a scale from 0 to 100 how stressful, challenging and unpleasant they had experienced the manipulation. Next, blood pressure and pulse measurements, saliva samples and subjective mood ratings were taken again.

Five minutes after the end of the TSST/control manipulation, when stress-induced cortisol was expected to peak, memory system engagement was assessed in a retrieval version of the PCL task. This retrieval version was identical to the learning task, except that no feedback was presented in order to prevent further learning and thus enabling us to specifically assess the recruitment of multiple memory systems during retrieval. Participants completed 100 trials of the retrieval task. After the retrieval phase, another measurement of blood pressure and pulse, another saliva sample and subjective mood assessment were taken. Finally, participants were debriefed. After testing, the saliva samples were stored at − 18 °C until analysis. Free cortisol concentrations were analyzed from saliva samples when data acquisition was completed

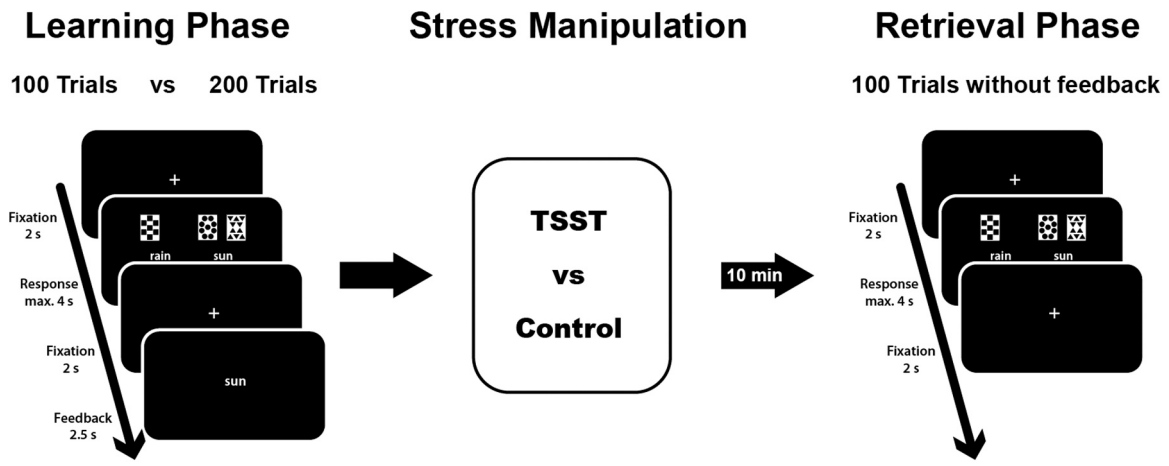

Fig. 1. Experimental procedure. In the learning phase, participants completed either 100 trials (moderate training) or 200 trials (intensive training) of the PCL task. Next, they underwent either a stress-induction protocol (Trier Social Stress Test, TSST) or a non-stressful control procedure. After the manipulation, all participants completed a retrieval version of the PCL task, consisting of 100 trials without feedback.

using a chemoluminescence immunoassay (IBL International, Hamburg, Germany). All inter- and intra-assay coefficients of variance were < 8%.

2.2.1. Strategy analysis

Memory system engagement can be inferred on the behavioral level from the use of different strategies in the PCL task (Gluck et al., 2002). Specifically, simple 'single-cue' strategies have been associated with the engagement of the hippocampus-dependent 'cognitive' memory system, whereas more complex 'multi-cue' strategies indicate the engagement of the dorsal striatum-dependent 'habit' memory system (Knowlton et al., 1996; Shohamy et al., 2004b; Foerde et al., 2006; Schwabe and Wolf, 2012). The strategies used by the participants were assessed by comparing participants' actual responses to the ideal responses predicted by the different strategies. Using least-square estimates, a fit score was derived for each strategy ranging from 0 to 1, with 0 indicating a perfect fit. The strategy with the lowest fit score was determined as the best-fitting strategy, thereby categorizing participants as single- and multi-cue users, respectively. If none of the fit scores was < 0.15, the strategy was considered unidentifiable, in line with previous studies using the same paradigm (Wirz et al., 2017; Zerbes et al., 2019, 2020b). Across the first 100 trials, 25.23% of the participants used no identifiable strategy, which did not differ between the four experimental groups ($\chi^2(3,\ N = 111) = 1.378$; $p = .711$; *Cramer's* $V = 0.111$). Across the second 100 trials (which were only completed by participants in the intensive training group), the proportion of unidentified strategies was 3.61%. We compared the proportion of unidentified strategies between groups across the second 100 trials using fisher's exact test (Fisher, 1934), as the expected values in each cell were too low for a standard χ^2-test. The stress and control groups did not differ in the proportion of unidentified strategies ($p = .110$).

Although the best-fitting strategies have been successfully used to assess multiple memory system engagement in previous studies (Gluck et al., 2002; Schwabe and Wolf, 2012; Wirz et al., 2017), categorizing participants in single- or multi-cue users might overlook more subtle differences between participants. Therefore, we recently introduced an additional measure that is computed as the difference between the fit scores for the single- and multi-cue strategies ($Fit_{single\text{-}cue} - Fit_{multi\text{-}cue}$) and referred to as 'Strategy Dominance Score' (Zerbes et al., 2020a; 2020b). This score takes into account that multiple memory systems may be active in parallel and reflects the relative dominance of one strategy over the other, with positive values indicating dominance of the multi-cue strategy and negative values indicating dominance of the single-cue strategy.

2.3. Control variables

In order to control for potential group differences in chronic stress, state and trait anxiety as well as depressive mood, participants completed the Trier Inventory for the Assessment of Chronic Stress (TICS, Schulz and Schlotz, 1999), the State-Trait Anxiety Inventory (STAI, Spielberger and Sydeman, 1994) and the Beck Depression Inventory (BDI_II, Beck et al., 1961). All questionnaires were completed before the testing day, except for the STAI state questionnaire, which was completed immediately before testing.

2.4. Data analysis

Subjective and physiological data were analyzed by means of mixed-design ANOVAs with the between-subject factors treatment (stress vs. control) and extent of practice (moderate vs. intensive) and the within-subjects factor time point of measurement. For classification performance during learning of the PCL task, the first 100 trials were analyzed with a mixed-design ANOVA with the between-subjects factors treatment (stress vs. control) and training (moderate vs. intensive) and blocks of 10 trials as within-subject factor. In addition, for the intensive practice group, classification performance was analyzed for the remaining 100 trials with only the between-subjects factor treatment (stress vs. control) and blocks of 10 trials as within-subjects factor. The strategy dominance score during learning was analyzed similar to the classification accuracy, except that the task was divided in blocks of 50 trials.

In the retrieval phase, the change in classification performance and strategy dominance score relative to learning was assessed by means of a mixed-design ANOVA with the between-subject factors treatment (stress vs. control) and extent of practice (moderate vs. intensive) and the within-subject factor phase (learning vs. retrieval). In this analysis, we used the last 50 trials of the learning phase as a measure for learning performance and strategy at the end of learning. To further examine the role of the physiological stress response in the stress-induced modulation of multiple memory systems during retrieval, we conducted a multiple linear regression model within the stress group with the strategy dominance score during retrieval as criterion. We included the predictors salivary cortisol (measurement 15 min after stress onset), systolic blood pressure (as indicator for autonomic arousal, using the measurement during the TSST), training condition as well as all possible interactions. In addition, we included the strategy dominance score across the last 50 trials of the learning phase as a predictor of no interest to control for potential baseline differences in strategy preference.

While our analyses focused on the strategy dominance score, we also

analyzed the best-fitting strategy for both learning and retrieval with either χ^2-tests (for analyzing between-subject effects) or McNemar tests (for analyzing within-subject effects). In addition, to control for possible baseline differences in strategy use during learning, we conducted logistic regression models for the best-fitting strategy during retrieval with the predictors treatment, training and learning strategy in the last 50 trials. All reported p-values are two-tailed. In case of violations of the sphericity assumption, Greenhouse-Geisser corrections were applied. All statistical analyses were carried out using R (version 3.5.2, R Core Team, 2018).

3. Results

3.1. Successful classification learning

Over the course of the first 100 learning trials, classification performance increased significantly from 49% to about 69% correct classifications (Fig. 2A, $F(6.42,686.43) = 15.30$; $p < .001$; $\eta^2_G = .686$). There were no differences between the moderate and intensive training groups in the first 100 trials of the learning phase (no significant main effects or interactions: all $F < 0.75$; all $p > .593$; all $\eta^2_G < 0.004$). Over the course of the second 100 learning trials in the intensive training group, classification performance did not further improve relative to the first 100 trials ($F(9423) = 0.83$; $p = .587$; $\eta^2_G = .008$). However, in the last 50 training trials (i.e. trials 50–100 in the moderate training group and trials 150–200 in the extensive training group), participants in the extensive training group showed significantly better classification performance than participants in the moderate training group ($F(1107) = 6.38$; $p = .013$; $\eta^2_G = .056$), suggesting that, as expected, the training manipulation led to superior performance in the intensive training group at the end of learning.

Both in the first as well as in the second 100 trials of training, there was a significant treatment × block interaction (both $F > 2.14$; both $p < .025$; both $\eta^2_G > 0.012$), suggesting that the stress group tended to perform lower at the beginning but better in the second half (Fig. 2A). This difference cannot be due to a treatment effect because the learning phase took place before the TSST/control manipulation. Importantly, comparing the performance between groups over the last 50 learning trials revealed no difference between the stress and control groups ($F(1,107) = 1.84$; $p = .177$; $\eta^2_G = .017$), showing that the groups reached comparable levels of performance at the end of training.

3.2. Practice-dependent shift from 'cognitive' to 'habit' learning

Memory system engagement in the PCL task can be inferred from the use of behavioral strategies (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004a). Across learning, 72% of the participants used single-cue strategies, indicating an overall predominance of 'cognitive' memory system engagement. The strategy dominance score, indicating the relative memory system preference, increased over the course of the first 100 trials (Fig. 2B, $F(2.80,299.59) = 9.36$; $p < .001$; $\eta^2_G = .039$), suggesting a relative shift towards 'habit' system engagement across learning, as observed before (Iaria et al., 2003; Zerbes et al., 2019; 2020b). There were no further effects of treatment or training condition in the first 100 trials, except for a non-significant trend for a treatment × block interaction ($F(2.80,299.59) = 2.58$; $p = .058$; $\eta^2_G = .011$, all other $F < 0.36$; all other $p > .148$; all other $\eta^2_G < .008$). In the second 100 trials, there was no significant main effect of block or a treatment × block interaction (both $F < 0.71$; both $p > .548$, both $\eta^2_G < 0.007$). When comparing the last 50 trials of training, the strategy dominance score did not differ between stress and control groups ($F(1,107) = 0.25$; $p = .620$; $\eta^2_G = .002$), suggesting comparable engagement of multiple memory systems between the groups at the end of training. There was, however, a significant effect of the extent of training on the used learning strategy. The intensive training group showed a higher strategy dominance score compared to the moderate training group over the last 50 trials of learning ($F(1,107) = 5.23$; $p = .024$; $\eta^2_G = .047$), suggesting that extensive training led to a stronger preference for multi-cue strategies, indicating engagement of the 'habit' memory system.

The best-fitting strategy did not change over the first 100 trials (Fig. 2C, $\chi^2(1, N = 56) = 2.57$; $p = .109$; *Odd's Ratio* = 2.50) nor over the remaining 100 trials in the intensive training group ($\chi^2(1, N = 39) = 0.00$; $p = .999$; *Odd's Ratio* = 1). At the end of learning, across the last 50 trials, the best-fitting strategy did not differ between the training groups ($\chi^2(1, N = 87) = 0.83$; $p = .363$; *Cramer's V* = 0.098). However, the stress group used significantly more multi-cue strategies across the last 50 trials compared to the control group ($\chi^2(1, N = 87) = 5.18$; $p = .023$; *Cramer's V* = 0.244). In order to account for these baseline differences between the stress and control groups, the learning strategy was included as a predictor into models examining the effects of treatment and training on the best-fitting strategy during retrieval.

3.3. Successful stress induction

3.3.1. Physiological measures

The effectiveness of the stress/control manipulation was demonstrated by significant changes in blood pressure, pulse, and salivary cortisol (Fig. 3A-C). Stress elicited significant increases in systolic and diastolic blood pressure as well as pulse (treatment × time interaction:

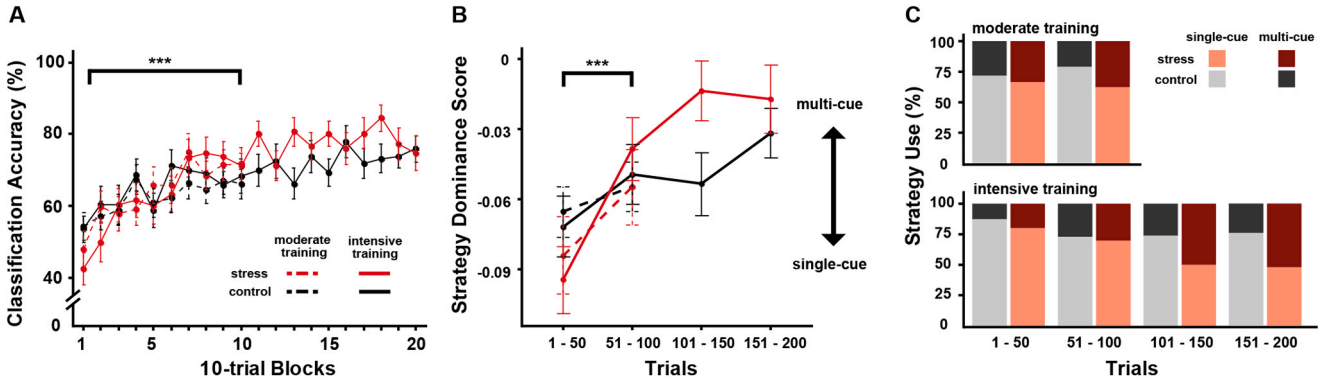

Fig. 2. Learning accuracy and strategy. (A) Across the first 100 trials of learning, classification performance increased significantly, suggesting successful task acquisition. Classification performance did not improve further over the second 100 trials in the intensive training group. (B) Over the course of the first 100 trials, the strategy dominance score increased, indicating increased 'habit' memory system engagement. There was no further change in the strategy dominance score across the second 100 trials in the intensive training group. (C) The best-fitting strategy revealed that both strategies were utilized, with an overall preference of the single-cue strategy. Strategy use indicated by the best-fitting strategy did not change significantly over the course of learning. Error bars denote standard error of the mean. ***$p < .001$.

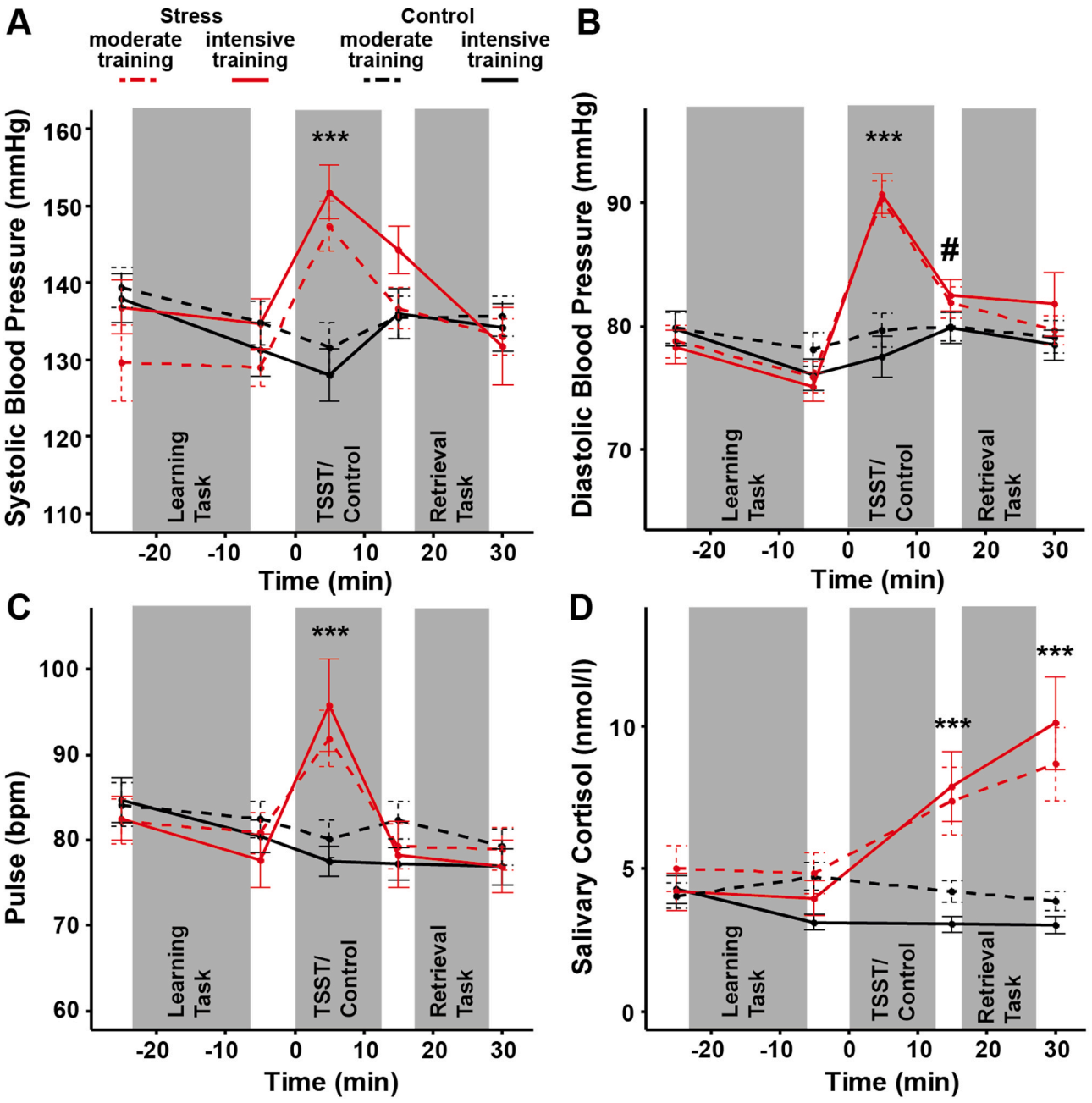

Fig. 3. Successful stress induction. Stress led to significant increases in (A) systolic blood pressure, (B) diastolic blood pressure, (C) pulse, and (D) salivary cortisol concentrations. Error bars denote standard error of the mean. Stress vs. control: ***$p < .001$; # $p < .10$.

all $F > 28.20$; all $p < .001$; all $\eta^2_G > 0.066$). Specifically, blood pressure and pulse did not differ between the stress and control groups before the manipulation (all $t < 1.56$; all $p > .122$). During the manipulation, however, blood pressure and pulse were significantly increased in the stress group compared to the control group (all $t > 4.34$; all $p < .001$). After the manipulation, this difference rapidly disappeared for systolic blood pressure and pulse (both $t < 1.55$; both $p > .125$), while the stress-induced increase in diastolic blood pressure tended to remain ($t(107.20) = 1.79$; $p = .078$). After the retrieval task, the stress and control groups did not differ in blood pressure or pulse (all $t < 1.12$; all $p > .267$). There was no significant effect of the extent of training on blood pressure or pulse (no main effects or interactions: all $F < 1.90$; all $p > .149$; all $\eta^2_G < 0.009$).

Stress led further to significant increases in salivary cortisol concentrations ($F(1.44,151.26) = 32.13$; $p < .001$; $\eta^2_G = .081$). While the stress and control groups showed comparable cortisol concentrations before the manipulation (both $t < 0.78$; both $p > .439$), salivary cortisol was significantly increased in the stress group compared to the control group after the manipulation ($t(58.69) = 4.46$; $p < .001$) and remained elevated until the end of the retrieval task ($t(54.12) = 5.59$; $p < .001$). Salivary cortisol levels were not affected by the training condition (no main effects or interactions: all $F < 1.74$; all $p > .187$; all $\eta^2_G < 0.006$).

3.3.2. *Subjective ratings*

Participants in the stress group rated the manipulation as significantly more stressful, challenging and unpleasant compared to the control group (all $F > 90.90$; all $p < .001$; all $\eta^2_G < 0.462$, Table 1). These ratings were unaffected by the training condition (no main effect or training × treatment interaction: all $F < 1.10$; all $p > .296$; all $\eta^2_G < 0.010$).

Table 1
Subjective stress responses and control variables.

	STRESS/ MOD	STRESS/INT	CON/ MOD	CON/INT
Subjective rating				
challenging	68.89 (4.54) ***	73.91 (4.61) ***	28.29 (3.59)	32.40 (4.63)
unpleasant	68.89 (5.07) ***	71.74 (5.89) ***	22.00 (3.01)	19.60 (3.98)
stressful	69.63 (4.12) ***	70.00 (4.95) ***	26.86 (3.54)	19.20 (3.10)
Positive subjective mood				
baseline	30.37 (1.14)	31.48 (0.90)	32.00 (1.12)	30.00 (1.33)
pre-treatment	27.22 (1.36)	24.00 (1.50)	29.89 (1.24)	26.20 (1.43)
post-treatment	27.15 (1.39) *	27.61 (1.53)	32.17 (1.28)	30.16 (1.31)
post-retrieval	26.26 (1.67)	25.61 (1.38)	29.77 (1.28)	28.72 (1.78)
Negative subjective mood				
baseline	12.74 (0.78)	12.65 (0.54)	13.51 (0.85)	13.32 (0.81)
pre-treatment	13.26 (0.66)	14.83 (1.56)	14.20 (0.81)	12.76 (0.73)
post-treatment	19.89 (1.66) ***	20.43 (1.64) ***	13.09 (0.69)	11.48 (0.40)
post-retrieval	14.52 (0.82)	15.17 (1.19) *	13.09 (0.64)	11.80 (0.62)
Depressive mood (BDI)	6.48 (1.37)	8.09 (1.50)	7.46 (1.11)	5.44 (0.86)
State anxiety (STAI-S)	34.48 (1.50)	36.52 (1.12)	34.83 (7.92)	35.00 (1.53)
Trait anxiety (STAI_T)	36.56 (1.73)	37.61 (1.74)	38.86 (1.47)	36.40 (1.34)
Subjective chronic stress (TICS)	12.74 (1.66)	12.70 (1.91)	14.83 (1.52)	13.56 (1.60)

Data represent mean (standard error of the mean). Asterisks denote difference between stress and control groups:
* $p < .05$;
*** $p < .001$

Subjective positive mood decreased over time ($F(3,318) = 19.93$; $p < .001$; $\eta^2_G = .045$, Table 1) and was overall significantly lower for the stress group compared to the control group ($F(1,106) = 4.43$; $p = .038$; $\eta^2_G = .030$). Furthermore, the change in positive mood over time was modulated by treatment ($F(3,318) = 4.17$; $p = .006$; $\eta^2_G = .010$). Specifically, at the start of the experiment, the groups showed comparable positive mood ratings ($t(107.66) = 0.25$; $p = .801$). Immediately before the manipulation, positive mood tended to be decreased in the stress group compared to the control group ($t(105.36) = 1.86$; $p = .066$). However, for both measurements after the manipulation, positive mood was significantly decreased in the stress group compared to the control group (both $t > 2.23$; both $p < .028$). In addition, the change in positive mood was modulated by training condition ($F(3,318) = 2.95$; $p = .033$; $\eta^2_G = .007$). This effect was driven by a significantly decreased positive mood in the intensive training group compared to the moderate training group at the measurement point after the learning task ($t(101.87) = 2.57$; $p = .011$), while the groups did not differ for the other measurement time points (all $t < 0.74$; all $p > .459$). The decreased subjective mood after learning in the intensive training group is likely explained by the longer task duration in that group, which might be experienced as exhausting. There were no further main effects or interactions on positive mood (all $F < 1.47$; all $p > .228$; all $\eta^2_G < 0.010$).

Negative mood ratings increased over time ($F(2.63,278.95) = 14.76$; $p < .001$; $\eta^2_G = .051$) and were significantly higher in the stress group compared to the control group ($F(1,106) = 11.25$; $p = .001$; $\eta^2_G = .062$). Moreover, the change in negative mood over time was modulated by treatment ($F(2.63,278.95) = 32.91$; $p < .001$; $\eta^2_G = .106$). Specifically, negative mood did not differ between the stress and control groups before the manipulation (both $t < 0.96$; both $p > .341$), but was significantly increased in the stress group compared to the control group after the manipulation (both $t > 2.72$; both $p < .008$). Negative mood was not affected by training (no main effects or interactions: all $F < 1.53$; all $p > .219$; all $\eta^2_G < 0.009$).

3.4. Stress promotes the use of 'habit' strategies after moderate but not intensive training

Classification performance further improved from the last 50 trials of learning to retrieval ($F(1,107) = 5.45$; $p = .021$; $\eta^2_G = .006$, Fig. 4A), reaching an overall accuracy of 74% correctly classified trials during retrieval. The intensive training group achieved a higher retrieval accuracy than the moderate training group ($F(1,107) = 4.21$; $p = .043$; $\eta^2_G = .038$), showing that the effects of the training manipulation on classification accuracy lasted during retrieval. In addition, classification performance was significantly higher in the stress group compared to the control group ($F(1,107) = 4.78$; $p = .031$; $\eta^2_G = .043$). However, when including the learning accuracy in the last 50 trials as covariate and thereby controlling for baseline differences between groups, the effect was reduced to a trend ($F(1,107) = 3.11$; $p = .081$; $\eta^2_G = .028$). Therefore, the effect of treatment on retrieval accuracy can be largely attributed to baseline differences between the stress and control groups during the training session.

Comparing the strategy dominance score in the last 50 trials of learning with the retrieval task revealed higher scores in the intensive training group compared to the moderate training group across phases ($F(1,107) = 4.72$; $p = .032$; $\eta^2_G = .035$, Fig. 4B), suggesting that the preference for 'habit' system engagement in the intensive training group overall persisted during retrieval. Most interestingly, however, the change in the strategy dominance score from learning to retrieval was modulated by treatment (treatment × phase interaction: $F(1,107) = 4.68$; $p = .033$; $\eta^2_G = .007$) and this effect was further accompanied by a significant three-way interaction training × treatment × phase ($F(1,107) = 4.40$; $p = .038$; $\eta^2_G = .007$). We examined this interaction by comparing the change in the strategy dominance score from learning to retrieval between the stress and control groups, separately for each training condition. In the moderate training group, the stress group showed a relative shift towards multi-cue strategies from learning to retrieval compared to the control group, indicating a stress-induced relative preference for 'habit' strategies ($t(52.90) = 2.69$; $p = .010$). However, in the intensive training group there was no effect of stress on the change in strategy dominance scores from learning to retrieval ($t(46.98) = 0.13$; $p = .890$), suggesting that extensive training made retrieval less sensitive to stress-induced changes.

For the best-fitting strategy, the single-cue strategy constituted about 58% of all identifiable strategies, which did not significantly differ from the end of learning ($\chi^2(1, N = 81) = 1.19$; $p = .275$; *Odd's Ratio* = 1.635). We analyzed the best-fitting strategy using logistic regression models with the predictors treatment and training as well as their interaction. In order to control for any baseline differences in strategy use, we also added the learning strategy in the last 50 trials as a predictor of no interest. However, this model did not provide a higher fit compared to a model including only the learning strategy as a predictor ($\chi^2(3) = 0.03$, $p = .999$), suggesting that the best-fitting strategy during retrieval was not affected by treatment or extent of training (all $\beta < 0.04$, all $z < 0.17$, all $p > .864$).

3.5. Role of autonomic arousal and cortisol in the recruitment of multiple memory systems during retrieval depending on training intensity

To further elucidate the mechanisms involved in the stress-induced modulation of memory system engagement during retrieval, we examined whether the retrieval strategy was linked to stress-induced elevations of salivary cortisol or autonomic arousal. To this end, we

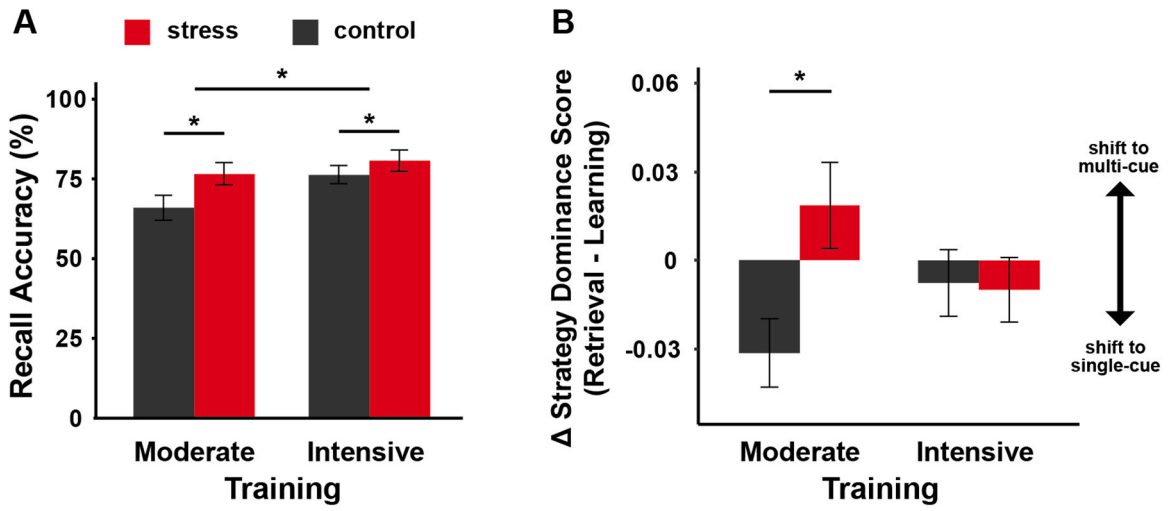

Fig. 4. Retrieval accuracy and strategy. (A) Retrieval performance was significantly increased in the intensive training group compared to moderate training. In addition, the stress group achieved significantly higher retrieval accuracies than the control group. However, this effect was not significant anymore ($p = .081$), when the accuracy at the end of learning was included as a covariate. (B) After moderate training, stress led to a shift in relative strategy dominance from learning to retrieval in favor of multi-cue strategies, indicating 'habit' memory system engagement. Error bars denote the standard error of the mean. * $p < .05$.

constructed a multiple regression model within the stress group with the strategy dominance score during retrieval as criterion. As predictors we included the salivary cortisol peak, the peak in systolic blood pressure, the training condition as well as all possible interactions between these variables. Furthermore, we included the strategy dominance score in the last 50 trials of the learning phase as a predictor of no interest, thereby controlling for differences in strategy use at baseline. The model overall provided a good fit to the data ($F(8,42) = 8.20$; $p < .001$; $R^2_{Adj} = .535$). For the individual predictors, there was a significant interaction between systolic blood pressure and training condition ($\beta = 0.29$; $t(102) = 2.83$; $p = .007$). We pursued this interaction by constructing separate models for the moderate and intensive training conditions, including the predictor systolic blood pressure and controlling for learning strategy. In the intensive training group there was no significant association of systolic blood pressure and the strategy dominance score during retrieval ($\beta = 0.13$; $t(21) = -0.94$; $p = .359$). However, there was a trend for a positive association in the moderate training group ($\beta = .28$; $t(24) = 1.72$; $p = .098$), suggesting that the stress-induced elevation of autonomic arousal tended to be associated with a relative preference for multi-cue strategy use after low-intensity training. Apart from that, the strategy dominance score during retrieval was also on trend-level interactively modulated by salivary cortisol and systolic blood pressure ($\beta = 0.20$; $t(102) = 1.69$; $p = .098$). We resolved this interaction by performing a median-split for the salivary cortisol level (median = 5.82) and conducted separate regression models for the resulting subsamples. This analysis showed that systolic blood pressure tended to be positively associated with the strategy dominance score for cortisol levels above the median ($\beta = 0.28$; $t(22) = 1.95$; $p = .064$), while there was no significant association when cortisol levels were low (i.e., below the median; $\beta = 0.18$; $t(22) = -1.10$; $p = .284$). In other words, concurrent elevations of salivary cortisol and systolic blood pressure after stress tended to be associated with a relative preference for multi-cue strategies during retrieval. However, as these associations did not reach statistical significance, they need to be interpreted with caution.

3.6. Control variables

There were no differences in depressive mood, chronic stress levels, or state and trait anxiety between any of the groups (all $F < 2.13$; all $p > .147$; all $\eta^2_G < 0.020$, Table 1).

4. Discussion

It is by now well-established that stress favors 'habit' over 'cognitive' memory systems during memory formation (Packard and Goodman, 2012; Vogel et al., 2016; Wirz et al., 2018). There is also accumulating evidence that stress may modulate the engagement of multiple memory system during retrieval, yet whether stress favors 'cognitive' or 'habit' memory during retrieval remained inconclusive (Elliott and Packard, 2008; Zerbes et al., 2019, 2020a, 2020b). The present study aimed to elucidate whether differences in the extent of initial training may modulate how stress affects the control of subsequent retrieval. Our results show that the extent of practice had indeed a critical impact on how stress biased memory system during retrieval. More specifically, our results showed that stress after moderate training increased the reliance on 'habit' memory retrieval, whereas after prolonged training, stress had no significant effect on which memory system guided retrieval.

With intensive training, participants not only achieved higher classification accuracy compared to moderate training, but also showed an increasing preference for using the multi-cue strategy, indicating the engagement of the dorsal striatal 'habit' system. This training-dependent shift in memory system engagement is in line with previous research (Poldrack et al., 2001; Chang and Gold, 2003; Iaria et al., 2003). Here, we show for the first time that the control of later memory retrieval is differentially affected by stress depending on the extent of training. After moderate training, stress led to a relative shift towards the use of multi-cue strategies, indicative of the 'habit' system, during retrieval, in line with previous reports in rodents (Elliott and Packard, 2008) and humans (Zerbes et al., 2020b). Further, the present results extend previous work suggesting that stress may promote 'habit' memory system engagement not only during learning (Kim et al., 2001; Schwabe and Wolf, 2012; Wirz et al., 2018), but also during later retrieval.

With prolonged training, however, stress did not affect the engagement of multiple memory systems during retrieval in the present study. The absence of a stress-induced modulation of the control of memory retrieval after extended training may suggest that stronger memories become less sensitive to stressful events. However, previous studies from our lab showed that stress or stress mediators may even bias memory retrieval in favor of 'cognitive' strategies after extended training (Zerbes et al., 2019, 2020a). These studies employed an identical training protocol as used here in the intensive training condition, indicating that the effects of stress on memory system engagement during retrieval may

vary to some extent even when training intensity is held constant. A critical difference between our previous studies and the present study, however, is the delay between learning and retrieval. While the retrieval phase immediately followed learning in the present study, it was delayed by twenty-four hours in studies that reported a shift back to 'cognitive' strategies during retrieval under stress or after administration of stress mediators (Zerbes et al., 2019, 2020a). This delay allowed for (presumably sleep-dependent) offline consolidation processes, which can change memory system balance (Zerbes et al., 2019). These altered memories may be sensitive to disruptive effects of stress and stress hormones on dorsal striatal memories (Guenzel et al., 2013; Atsak et al., 2016). In order to avoid such time-dependent dynamics in the present study and to specifically investigate the role of training intensity, learning and retrieval phases were realized shortly one after another, on one experimental day. As a consequence, however, it may be difficult to strictly separate stress effects on early consolidation and memory retrieval in the present study. This issue could be addressed in future studies using longer delays between learning and retrieval.

How can the training-dependent effect of stress on the control of memory retrieval be explained? One explanation may be related to the training-dependent strength of 'cognitive' and 'habit' memory systems. After moderate training, behavior is predominantly governed by the 'cognitive' memory system, while the 'habit' memory trace is still weak (Poldrack et al., 2001; Chang and Gold, 2003). At this stage, stress may affect the control of memory retrieval similar to memory formation by promoting 'habit' memory system engagement (Kim et al., 2001; Schwabe and Wolf, 2012; Wirz et al., 2017). In line with this view, we showed recently that stress before retrieval increases indeed the activity of the dorsal striatum (Zerbes et al., 2020b). However, extended training gradually shifts control towards the dorsal striatal 'habit' memory system (Poldrack et al., 2001; Iaria et al., 2003). This may preclude further stress-induced enhancements of 'habit' memories during subsequent retrieval. This view is supported by our present finding that behavioral strategies indicative for the 'habit' system were indeed significantly more often engaged after extended than after moderate training.

Interestingly, the stress-induced shift towards a preferential engagement of the 'habit' memory system after moderate training tended to be associated with the stress-induced elevation of autonomic arousal. Noradrenergic arousal has been shown to play an important role in the stress-induced modulation of multiple memory systems (Packard and Wingard, 2004; Wirz et al., 2017), most likely by acting on the amygdala, which in turn modulates hippocampal and dorsal striatal systems (Vogel et al., 2016), as described for quantitative changes in consolidation and retrieval (Roozendaal et al., 2003, 2006b). Apart from the effect of noradrenaline, glucocorticoids are also known the play a critical role in stress-induced changes in memory system engagement during learning (Schwabe et al., 2010a; Schwabe et al., 2013; Vogel et al., 2016, 2017). Although stress-induced cortisol was not significantly linked to strategy use in the present study, there was a trend-level interaction of stress-induced elevations of cortisol and autonomic arousal. Interactive effects of cortisol and noradrenergic arousal are well-established for stress effects on memory consolidation and memory retrieval per se (Roozendaal et al., 2004, 2006b; de Quervain et al., 2007) and have also been shown to modulate different brain systems in the control of instrumental learning (Schwabe et al., 2010b, 2012b). The present findings suggest that concurrent increases in glucocorticoids and noradrenergic arousal may be associated with a relative preference of 'habit' memory system engagement during retrieval. This idea of an interactive influence of noradrenergic arousal and glucocorticoids on the control of memory retrieval is further in line with a recent pharmacological study from our lab indicating that a beta-adrenergic receptor antagonist prevented stress effects on the control of memory retrieval (Zerbes et al., 2020a). However, the results linking memory system engagement during retrieval to elevations in salivary cortisol and autonomic arousal in the present study need to be interpreted with great caution, as they are based on statistically non-significant trends.

The present results suggested that classification accuracy in the PCL task was not impaired after stress, in line with previous results for both learning (Schwabe and Wolf, 2012; Schwabe et al., 2013) and retrieval (Zerbes et al., 2020a, 2020b). This stands in contrast to previous studies showing that stress hampers memory retrieval. However, this stress-induced retrieval deficit is typically found in tasks depending either on hippocampal or dorsal striatal memory alone, in which one system can hardly replace the other (de Quervain et al., 1998; Diamond et al., 2006; Schwabe et al., 2012a; Guenzel et al., 2013; Atsak et al., 2016). Here, however, both the hippocampal 'cognitive' and the dorsal striatal 'habit' system could contribute to successful performance in the PCL task (Zerbes et al., 2020b), allowing for stress-induced adaptations in the utilized memory system, when memories were initially established in both systems. Such adaptations in memory system engagement may serve to buffer possible stress-induced impairments, as suggested before (Schwabe et al., 2010a, 2013). Thus, a retrieval deficit after stress may be primarily found if the task relies on a single memory system, for example by using a paired-associate learning version of the PCL task, which has been shown to depend to the 'cognitive' memory system (Poldrack et al., 2001; Shohamy et al., 2004a).

To conclude, the present study shows that the impact of acute stress on the balance of 'cognitive' and 'habit' memory during retrieval depends on the extent of initial training. We show that stress favors dorsal striatal 'habit' memory during retrieval only after moderate learning, whereas the balance of 'cognitive' and 'habit' memory during retrieval remained unaffected by stress when training was extensive. The present findings provide not only further evidence that stress may affect the nature of remembering by modulating the use of multiple memory systems during retrieval but show also when this stress effect is likely to occur and suggest that stress accelerates a shift that would otherwise occur after extended training.

Declarations of interest

None.

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