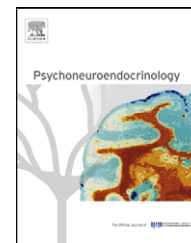




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Socially evaluated cold pressor stress after instrumental learning favors habits over goal-directed action

Lars Schwabe*, Oliver T. Wolf

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

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Summary Instrumental action can be controlled by two anatomically and functionally distinct systems: a goal-directed system that learns action–outcome associations and a habit system that learns stimulus–response associations without any link to the incentive value of the outcome. Recent evidence indicates that stress before learning modulates these two systems in favor of habitual control. Here, we examined the impact of a stress exposure after learning on instrumental performance. Participants learned to choose two instrumental actions that were associated with the delivery of different food rewards. After learning, one of these food rewards was devalued as participants were saturated with that food. Before being re-exposed to the instrumental actions in extinction, participants were subjected to the socially evaluated cold pressor test or a control procedure. Controls but not stressed participants reduced responding to the action associated with the devalued outcome. That is, acute stress before extinction testing abolished sensitivity of performance to outcome devaluation. Cortisol responses to stress correlated significantly with habitual performance. These findings show that stress induced by the socially evaluated cold pressor test can make behavior habitual without affecting processes involved in learning.

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Introduction

Instrumental action can be controlled by two distinct processes: a goal-directed process that involves learning of associations between actions and the incentive value of an

outcome (action–outcome learning), and a habit learning process that involves learning associations between contexts or stimuli and responses (stimulus–response learning) (Dickinson, 1985; Dickinson and Balleine, 1994). At a neural level, goal-directed and habitual processes are supported by distinct brain structures. Rodent studies indicated that goal-directed action relies on a neural network consisting of the medial prefrontal cortex, the dorsomedial striatum and the dorsomedial thalamus (Balleine and Dickinson, 1998; Corbit et al., 2003; Yin et al., 2005) whereas habits are mediated by the dorsolateral striatum (Yin et al., 2004, 2005). This

* Corresponding author. Tel.: +49 234 3229324;
fax: +49 234 3214308.

E-mail address: Lars.Schwabe@rub.de (L. Schwabe).

dissociation has been confirmed in human neuroimaging and neuropsychological studies (Knowlton et al., 1996; Valentin et al., 2007; Tricomi et al., 2009).

Based on a large body of literature demonstrating that stress, i.e. the real or perceived threat of an individual's homeostasis (McEwen, 2000), and the glucocorticoid stress hormones (cortisol in humans) modulate learning and memory processes (de Quervain et al., 1998; Buchanan et al., 2006; Payne et al., 2007); for reviews see (Roosendaal et al., 2009; Wolf, 2009), we asked in a recent study whether stress affects the use of goal-directed and habit systems in instrumental learning (Schwabe and Wolf, 2009). In this previous study, we used a devaluation paradigm (Balleine and Dickinson, 1998) and found that acute stress before learning rendered participants' action insensitive to changes in the value of the action goal. In other words: stress before learning made participants' behavior habitual.

While these findings provided the first demonstration of a stress-induced modulation of goal-directed and habitual systems in instrumental action, this study did not address which processes were influenced by stress. Stress preceded both learning and extinction testing and cortisol levels were still elevated after training (i.e. before extinction testing). Therefore, it remained unclear whether stress affected processes involved in either acquisition (e.g. attention, initial encoding) or performance (e.g. memory retrieval, response inhibition). If stress exerted its effect mainly on acquisition processes, then instrumental behavior should remain unaffected by a stress exposure after learning. If, however, stress affected primarily performance, then we should see the impairment in the goal-directedness of behavior also when subjects are stressed before extinction testing.

In the present experiment, we examined whether acute stress favors habits over goal-directed action when it is administered before the extinction test. Participants were first trained in two instrumental actions leading with a high probability to two distinct food outcomes. After training, we devalued selectively one of the two food outcomes by inviting subjects to eat that food to satiety. Then, participants were exposed to an acute, brief stressor (hand in ice water and social evaluation in the socially evaluated cold pressor test, SECP) or a non-stressful control condition, before they were tested in the two instrumental actions in extinction. Goal-directed behavior is expressed by a decrease in the frequency of the action associated with the devalued outcome, i.e. the food eaten to satiety.

Methods

Participants and design

Sixty-eight students of the Ruhr-University Bochum (34 men, 34 women) between 18 and 32 years of age ($M \pm SEM$: 23.4 ± 0.3 years) and with a body-mass-index between 19 and 28 kg/m^2 ($22.6 \pm 0.3 \text{ kg/m}^2$) participated in this study. The following exclusion criteria were checked in a standardized interview: any medical condition, current or lifetime psychopathology, use of medication, drug abuse, smoking, any food intolerance as well as current or planned diet. Women taking oral contraceptives were excluded from participation because oral contraceptives may change the neu-

roendocrine stress response (Kirschbaum et al., 1999). We tested women only in their luteal phase defined as the two weeks before menses as their stress responses in this phase of the menstrual cycle are most similar to those of men (Kirschbaum et al., 1999). Furthermore, we pre-screened participants to ensure that they find the presented foods (chocolate milk, chocolate pudding, oranges, orange juice, and peppermint tea) pleasant. Nevertheless, 17 subjects had to be excluded from analyses because they revealed during the experiment that they disliked at least one of the foods [pleasantness rating below 10 on a scale from 0 ("not pleasant") to 100 ("very pleasant")] and choosing the high probability action <20% of the time; see Valentin et al. 2007; Schwabe and Wolf, 2009].

Participants were asked to refrain from caffeine and physical exercise within the 6 h before testing and to fast for at least 3 h before the experiment started. Participants were told beforehand that they would participate in a study on stress and learning, i.e. they knew that they might be exposed to a stressor but they were not told about the nature of the learning task. All participants provided written informed consent for their participation. The experiment was reviewed and approved by the ethics committee of the German Psychological Society.

We used a between-subjects design in which participants were randomly assigned to the stress or control group. All testing took place between 1300 and 1700 to control for the diurnal rhythm in the secretion of the stress hormone cortisol. The experimental procedure is summarized in Fig. 1A.

Instrumental learning paradigm

The employed learning task was introduced recently by Valentin et al. (2007). In this task, participants completed three trial types: chocolate, orange, and neutral (see Fig. 1B). On each trial type, they were asked to choose one of two distinct symbols (presented on a computer screen) by clicking on it with the left mouse cursor. According to the reward schedule associated with the chosen action, they received 1 ml of a fluid or else no liquid was delivered. The liquids were delivered with separate pumps and transferred via 3-m-long tubes (diameter: 3 mm) to the participants who kept the ends of the tubes like a straw between their lips. Importantly, the two actions in each trial type differed regarding the probability with which an outcome was delivered. One action led to a food outcome with a probability of $p = 0.7$ (*high probability action*) whereas the probability for a food outcome was $p = 0.2$ for the other action (*low probability action*). On chocolate and orange trials, the high probability action was followed with a probability of $p = 0.5$ by chocolate milk and orange juice, respectively, and by peppermint tea with a probability of $p = 0.2$ (reward and common outcome were never presented on the same trial). The low probability action delivered peppermint tea with a probability of $p = 0.2$ but was never associated with chocolate milk or orange juice. In neutral trials, water was delivered, either with a probability of $p = 0.7$ (*high probability action*) or with a probability of $p = 0.2$ (*low probability action*). These neutral trials served as a control to assess the effect of the rewards (chocolate milk, orange juice) on participants' choice behavior.

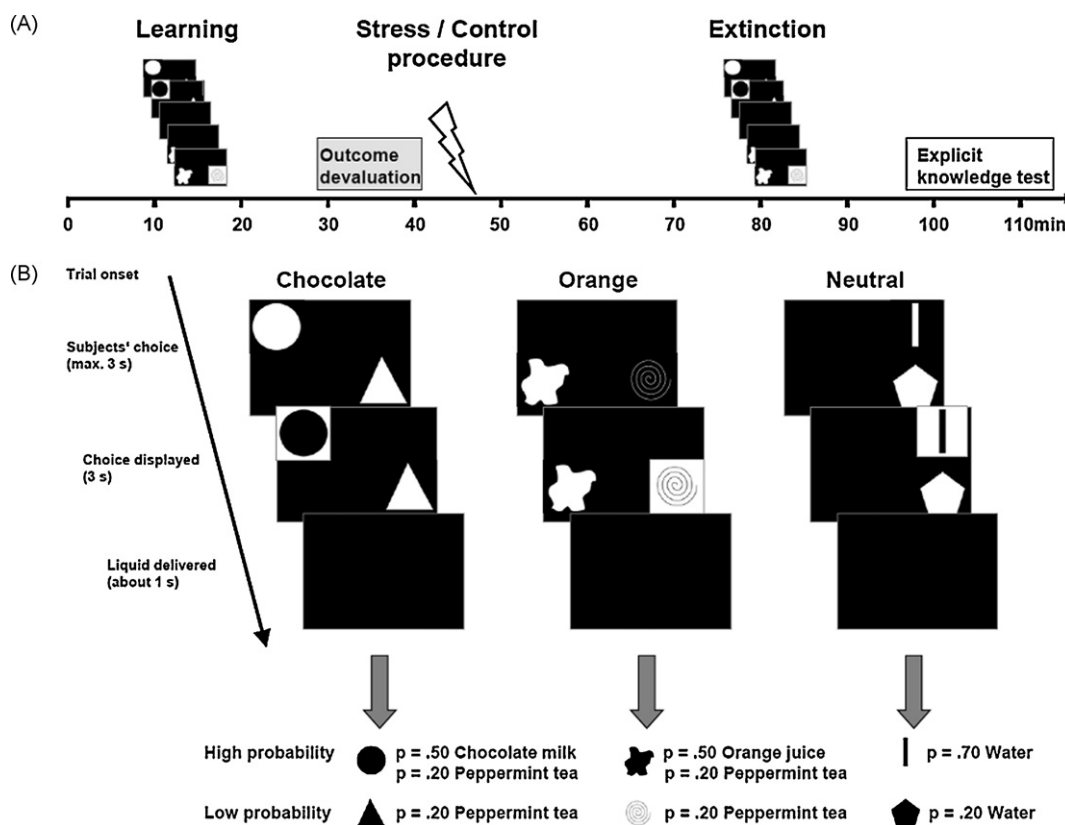


Figure 1 (A) Time line of the experiment. Participants were first trained in the instrumental task. After the selective outcome devaluation (satiation with oranges or chocolate pudding) but before the extinction test, subjects were exposed to stress (socially evaluated cold pressor test) or a control condition. (B) The instrumental task (reproduced with permission from the Society for Neuroscience). Participants completed three trial types (chocolate, orange, and neutral). In each trial type, there was one action that led with a high probability to a food outcome and one action that led with a low probability to a food outcome. Depending on the trial type, the high probability action yielded chocolate milk or orange juice with a probability of $p = 0.5$, a common outcome (peppermint tea) with a probability of $p = 0.2$, or nothing. The low probability action led to the common liquid with a probability of $p = 0.2$. After an action was chosen, the referring symbol was highlighted for 3 s before the food was delivered. During the extinction test, chocolate milk and orange juice were no longer presented.

After participants selected an action, the related symbol was highlighted for 3 s before – depending on the chosen action and the associated reward schedule – a liquid was delivered. Then, the screen was cleared and the next trial began. Participants completed 75 trials per trial type resulting in 225 trials in total (intertrial interval: ~ 8 s; processing time: ~ 30 min). The occurrence of the trial types was randomized. The specific assignment of the symbols and the spatial position to each action was counterbalanced across subjects.

Selective outcome devaluation

After the learning session, participants were invited to eat either as much chocolate pudding (Campina Optiwell; 150 g per cup; 55 kcal per 100 g) or as many oranges (40 kcal per 100 g) as they wanted. On average, participants ate 3 cups of chocolate pudding and 3 oranges, respectively; the amount of food consumed was comparable in the stress and control groups. This selective satiation should decrease the value of one food outcome (e.g. satiation with chocolate pudding should decrease the value of the chocolate milk) while the

value of the other food outcome (orange juice in the example) remains high. Which of the two food outcomes was devalued was counterbalanced across subjects.

Hunger and pleasantness ratings

To evaluate the influence of the selective satiation with either chocolate pudding or oranges, we collected subjects' ratings of hunger (from 0 "not hungry" to 100 "very hungry") and pleasantness of the liquids (from 0 "not pleasant" to 100 "very pleasant") before learning, before and immediately after the devaluation as well as immediately before the extinction session.

Stress protocol

After the outcome devaluation, participants in the stress condition (16 men, 12 women) were exposed to the socially evaluated cold pressor test (SECP) as described in detail elsewhere (Schwabe et al., 2008). In short, they had to immerse their right hand up to and including the wrist for 3 min into ice water ($0-2^{\circ}\text{C}$). During hand immersion they were videotaped and monitored by a rather cold and

unsociable experimenter. Participants were not told beforehand that this procedure should induce stress.

Participants in the control condition (12 men, 11 women) immersed their right hand up to and including the wrist for 3 min in warm water (35–37 °C). They were neither videotaped nor monitored during hand immersion. Subjective stress ratings, blood pressure and salivary cortisol concentrations were measured to assess whether the stress induction by the SECPT was successful.

Subjective stress ratings

Immediately after the SECPT or control condition, participants rated on a scale from 0 (“not at all”) to 100 (“very much”) how stressful, painful and unpleasant they experienced the previous situation.

Blood pressure

Blood pressure was measured before, during as well as after the SECPT or control condition by means of the Dinamap system (Critikon®, Tampa, FL) with the cuff placed at the left upper arm.

Salivary cortisol

We measured participants’ cortisol response to stress because (i) an increase in cortisol is a common measure of the effectiveness of a stress manipulation (e.g. Dickerson and Kemeny, 2004) and (ii) there are many studies showing that cortisol plays a crucial role in stress effects on cognition (de Quervain et al., 1998; Roozendaal et al., 2009).

Participants collected saliva samples with the help of Salivette (Sarstedt®, Germany) collection devices after arrival at the laboratory, immediately before, immediately after as well as 20 and 50 min after the SECPT or control condition. Saliva samples were stored at –20 °C until analyses. The biologically active, free fraction of the stress hormone cortisol was analyzed from saliva using an immunoassay (IBL, Hamburg). Inter- and intra-assay coefficients of variance were below 9 percent.

Extinction test

Twenty-five minutes after the cessation of the stress or control condition and about 40 min after the end of the learning session, participants completed again 75 trials of the three trial types in random order. This interval between the stress or control condition and the extinction test has been chosen because cortisol reaches peak levels about 25 min after stressor onset (Schwabe et al., 2008). Again, subjects selected an action by moving the mouse cursor to one of the symbols and pressing the left mouse button. Same as during learning, the symbol representing the chosen action was highlighted. This time, however, the rewards (chocolate milk, orange juice) were never delivered, i.e. subjects were tested in extinction for these outcomes. On the chocolate and orange trials, both actions led to peppermint tea with a probability of $p = 0.2$. In the neutral trials, both actions were followed by water with a probability of $p = 0.2$. This extinction procedure ensured that participants only use information about the value of the outcome by making use of the previously learned action–outcome associations.

Choosing the high probability action associated with the devalued food less often than during learning indicated goal-directed behavior. The ongoing choice of the devalued high probability action was interpreted as indicative for habitual behavior.

Assessment of explicit task knowledge

At the end of the experiment, we assessed participants’ explicit task knowledge. First, they were asked in a free recall test about the actions necessary to receive chocolate milk, orange juice or water (action–outcome associations). We gave one point for each correctly named symbol and symbol position (e.g. participants received two points if they mentioned correctly that they had to click with the mouse cursor at the circle in the left upper corner to receive chocolate milk), i.e. a maximum score of 6 points could be reached.

Following the free recall test, we presented participants a multiple choice questionnaire in which they had to indicate (i) which symbol was associated with chocolate milk, orange juice or water and (ii) the position of the six symbols presented in the three trial types. Participants received one point for each correct answer, i.e. 9 points if they answered all questions correctly.

Statistical analyses

Data were analyzed by means of ANOVAs, paired t -tests and t -tests for independent samples. In line with earlier studies using the same paradigm (Valentin et al., 2007; Schwabe and Wolf, 2009), learning and extinction test trials were divided in 5 five blocks with 15 trials per block. All reported p -values are two-tailed; p -values were Bonferroni corrected when indicated. We included the partial η^2 as a measure of effect size. According to the conventions by (Cohen, 1988) $\eta^2 = 0.01$ was considered a small effect and $\eta^2 = 0.06$ and $\eta^2 = 0.12$ as medium-sized and large effect, respectively.

Results

Instrumental learning

As training proceeded, subjects preferred increasingly the high probability actions associated with the food rewards (i.e. the non-devalued and the subsequently devalued foods) over their low probability counterparts (Fig. 2). However, participants did not favor the high probability action in the neutral trials indicating that they were indifferent as to whether they received the effectively neutral outcome or not. This conclusion was supported by a group (SECPT vs. control) \times sex (men vs. women) \times value (valued, devalued, neutral) \times time (five blocks with 15 trials per block) ANOVA yielding significant effects of time ($F_{(4,184)} = 16.15, p < .001, \eta^2 = 0.26$) and value ($F_{(2,92)} = 11.00, p < .001, \eta^2 = 0.19$) and a time \times value interaction ($F_{(8,368)} = 1.99, p < .05, \eta^2 = 0.05$).

Importantly, the learning curves of the SECPT and control groups did not differ (Fig. 2), nor was there an effect of participants’ sex or an interaction between these factors (all $F < 1.4$, all $p > .24$, all $\eta^2 < 0.03$).

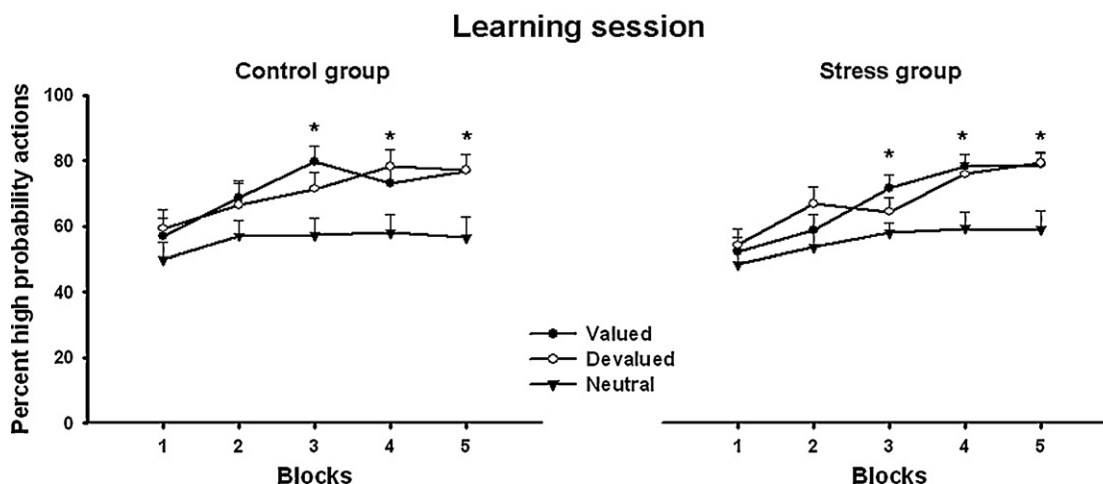


Figure 2 Learning curves in the instrumental task. Over training, all participants favored increasingly the high probability actions leading to the valued and subsequently devalued outcomes over their low probability counterparts (*Bonferroni-corrected $p < .05$) but were indifferent between high- and low probability actions in neutral trials. Data represent $M \pm SEM$.

Effects of selective outcome devaluation on hunger and food pleasantness

Feeding subjects to satiety with either chocolate pudding or oranges led to a significant decrease in subjective hunger ratings from 57 (± 3.22 SEM) before satiety to 28 (± 2.99 SEM) immediately after satiety and 36 (± 3.4 SEM) immediately before the extinction test ($F_{(2,90)} = 65.82$, $p < .001$, $\eta^2 = 0.59$). As shown in Fig. 3, pleasantness ratings decreased markedly for the food eaten to satiety (i.e. the devalued food) but not for the foods not eaten (value \times time interaction: $F_{(9,405)} = 41.19$, $p < .001$, $\eta^2 = 0.48$).

The changes in hunger and pleasantness ratings following the selective outcome devaluation were comparable in participants in the SECPT and control groups as well as in men and women (all $F < 2.3$, all $p > .13$, $\eta^2 < 0.05$).

Subjective and physiological changes in response to the SECPT

Subjective stress ratings and elevations in blood pressure and salivary cortisol indicated the successful stress induction by the SECPT.

All but seven participants (3 men, 4 women; mean duration = 91 s; range: 35–120 s) in the SECPT group immersed their hand for the full 3 min in ice water. Those subjects who took their hands earlier out of the water did not differ in their stress responses from the rest of the SECPT group (subjective stress ratings: all $t_{(25)} < 1.1$, all $p > .30$; systolic and diastolic blood pressure: all $F < 1.4$, all $p > .25$; salivary cortisol: all $F < 1.6$, all $p > .21$; see [supplementary Table 1](#)).

Subjective stress ratings

As expected, participants in the SECPT group experienced the experimental manipulation as significantly more stressful, painful and unpleasant than controls (all $F > 45$, all $p < .001$, all $\eta^2 > 0.50$; [Table 1](#)). Men and women did not differ in their subjective assessments; nor was there a

group \times sex interaction (all $F < 1$, all $p > .35$, all $\eta^2 < 0.02$).

Blood pressure

The SECPT but not the control condition caused a significant increase in systolic and diastolic blood pressure. [Table 1](#) shows that stressed and control subjects differed in their blood pressure during but neither before nor after hand immersion (group \times time: both $F > 45$, both $p < .001$, both $\eta^2 > 0.50$; time: both $F > 40$, both $p < .001$, both $\eta^2 > 0.45$; group: both $F > 3.8$, both $p \leq .05$, both $\eta^2 > 0.07$). Men had higher systolic blood pressure than women ($F_{(1,46)} = 38.55$, $p < .001$, $\eta^2 > 0.46$; diastolic blood pressure: $F_{(1,46)} = 2.73$, $p = .11$, $\eta^2 = 0.06$) but sexes did not differ in their blood pressure responses to the SECPT (group \times sex: both $F < 1$, both $p > .70$, both $\eta^2 < 0.01$).

Table 1 Subjective ratings of stressfulness, painfulness and unpleasantness as well as blood pressure values before, during and after hand immersion in the stress and control groups.

	Control group	Stress group
Subjective ratings		
Stressfulness	5.9 \pm 2.8	45.9 \pm 4.7*
Painfulness	1.4 \pm 1.0	70.0 \pm 3.7*
Unpleasantness	3.6 \pm 1.4	64.4 \pm 4.5*
Systolic blood pressure (mmHg)		
Before hand immersion	113.3 \pm 2.9	117.0 \pm 3.1
During hand immersion	109.7 \pm 2.9	132.6 \pm 3.6*
After hand immersion	109.6 \pm 3.1	113.8 \pm 2.8
Diastolic blood pressure (mmHg)		
Before hand immersion	64.0 \pm 1.2	62.5 \pm 1.4
During hand immersion	63.9 \pm 1.5	77.9 \pm 1.9*
After hand immersion	63.3 \pm 1.2	61.7 \pm 1.0

Subjective assessments were measured on a scale from 0 ("not at all") to 100 ("very much").

* Significant group difference ($p < .01$).

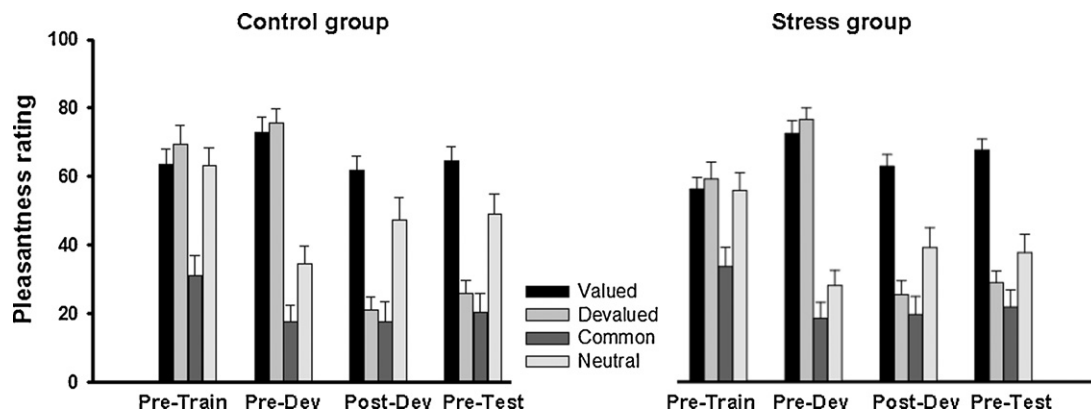


Figure 3 Pleasantness ratings on a scale from 0 (“not pleasant”) to 100 (“very pleasant”) for the valued, devalued, common and neutral food outcomes in the control and stress groups. Consistent with specific satiation, subjective pleasantness ratings decreased sharply for the devalued food but not for the valued food. The pleasantness ratings of stressed and control participants were comparable. Data represent $M \pm SEM$.

Salivary cortisol

Salivary cortisol increased significantly in response to the SECPT but not in response to the control condition (group \times time: $F_{(4,184)} = 5.10, p = .001, \eta^2 = 0.10$; time: $F_{(4,184)} = 6.05, p < .001, \eta^2 = 0.12$; group: $F_{(1,46)} = 3.47, p < .07, \eta^2 = 0.07$). Fig. 4 shows that groups differed in their cortisol levels 20 min after the SECPT/control condition, i.e. at the start of the extinction test ($t_{(49)} = 3.50, p = .001$). Men and women did not differ in their cortisol responses to the SECPT (sex: $F_{(1,46)} = 0.70, p = .41, \eta^2 = 0.02$; group \times sex: $F_{(1,46)} = 0.30, p = .59, \eta^2 < 0.01$).

Habitual and goal-directed performance in the extinction test

Twenty-five minutes after exposure to the SECPT (or the control condition), participants were presented the learned

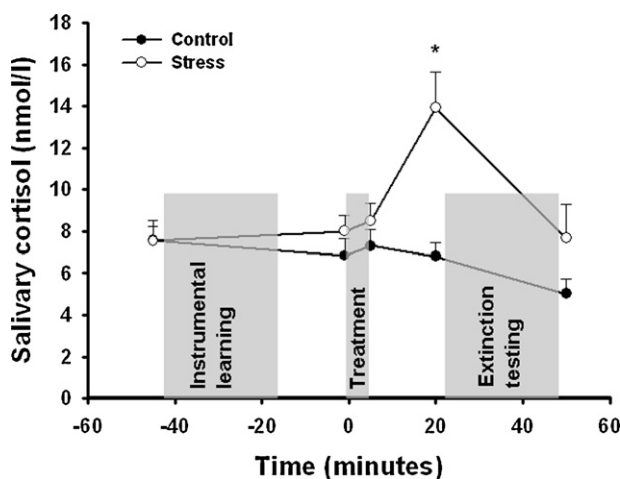


Figure 4 Salivary cortisol concentrations across the experiment. Cortisol concentrations were comparable in the stress and control groups during learning. Exposure to the SECPT led to a significant increase in salivary cortisol. Note that peak cortisol levels were reached immediately before testing. *Significant group difference ($p < .001$). Data represent $M \pm SEM$.

instrumental actions in extinction. Goal-directed behavior was reflected in a decrease in the choice of the action associated with the devalued outcome. Habit performance was indicated by the ongoing selection of the devalued instrumental action.

Participants’ choice behavior is shown in Fig. 5. We observed a clearly distinct choice pattern in SECPT stressed and control participants during extinction testing (group \times time \times value interaction: $F_{(8,368)} = 3.46, p = .001, \eta^2 = 0.07$). In the control group, participants chose the valued high probability action significantly more often than the devalued high probability action across extinction testing ($F_{(1,21)} = 5.91, p < .03, \eta^2 = 0.23$). They preferred the valued high probability action over its low probability counterpart in the first 15-trial block of the extinction test ($t_{(21)} = 7.74, p < .001$), before they could know that the valued outcome is no longer presented. However, participants in the control group did not favor the high probability action associated with the devalued outcome over the referring low probability action in the first extinction block. To the contrary, they tended to choose the low probability more often, i.e. they even avoided the devalued high probability action ($t_{(21)} = 1.95, p < .07$). In sum, control participants performed goal-directed: they did not prefer the devalued food any more, thus they did not prefer the associated action any more.

In contrast, SECPT stressed participants did not change their choice behavior following the selective outcome devaluation. They chose the devalued high probability action as often as the valued high probability action across the testing session ($F_{(1,26)} = 0.07, p = .79, \eta^2 < 0.01$). In the first 15-trial block, SECPT stressed participants favored both the high probability action associated with the valued outcome and the high probability action associated with the devalued outcome over the referring low probability actions (both $t_{(27)} > 6.5$, both $p < .01$). Thus, participants that were exposed to the SECPT before extinction testing performed habitually: they indicated that they do not want the devalued outcome any more but still chose the referring action.

All participants chose the high and low probability actions at random after the first 15-trial block, which suggests successful extinction learning.

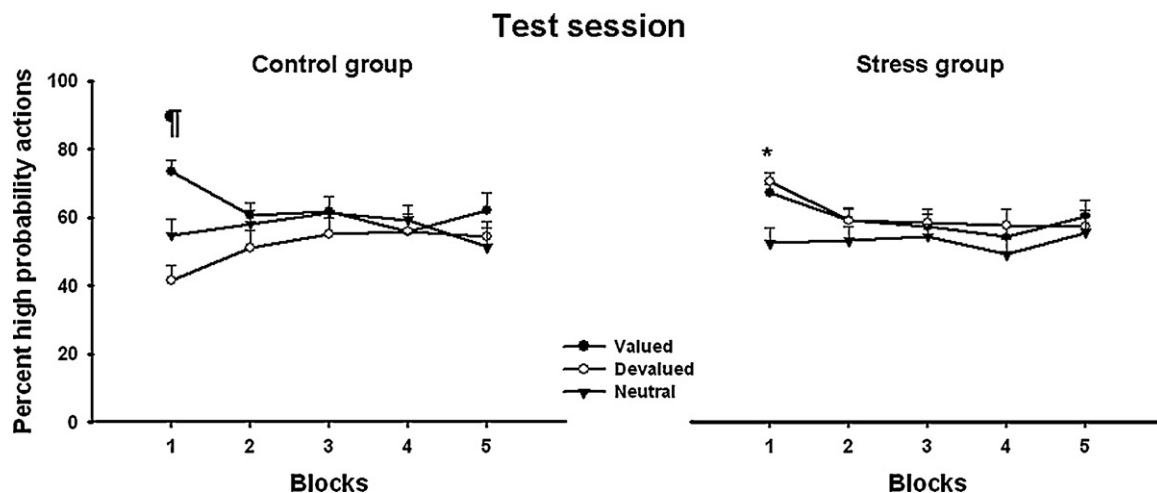


Figure 5 Percentage of high probability actions chosen in the five 15-trial blocks of the extinction test session. Participants in the control group preferred the valued but not the devalued instrumental action in the first block indicating that they modulated their instrumental responses following the change in the value of the associated food. In contrast, stressed participants favored both the valued and the devalued instrumental action in the first extinction block. Data represent $M \pm SEM$. ¶ valued high probability action favored over low probability counterpart ($p < .05$); *valued and devalued high probability actions favored over their low probability counterparts ($p < .05$).

As the SECPT stress effect on participants’ instrumental performance was most prominent in the first block of the extinction test, we contrasted the change in behavior from the last training block to the first extinction block in the stress and control groups (Fig. 6). In a group (SECPT vs. control) \times sex (men vs. women) \times value (valued vs. devalued) \times time (last 15 training trials vs. first 15 test trials) ANOVA we obtained a significant three-way interaction between group, value and time ($F_{(1,46)} = 13.61, p < .001, \eta^2 = 0.23$), indicating that controls ($F_{(1,21)} = 12.80, p < .001, \eta^2 = 0.39$) but not SECPT stressed participants ($F_{(1,26)} = 0.26, p = .61, \eta^2 = 0.01$) showed a decrease in responding to the devalued high probability action after selective outcome devaluation.

Interestingly, the increase in salivary cortisol from immediately before to 20 min after the SECPT exposure correlated

significantly with the number of devalued high probability choices in the SECPT group ($r = 0.57, p < .01$) indicating that higher cortisol responses to the SECPT were associated with more habitual behavior.

Participants’ sex had no effect on performance in the extinction test, nor did it interact with the stress manipulation (both $F < 1.3$, both $p > .25$, both $\eta^2 < 0.03$).

Effects of the SECPT on explicit knowledge

Explicit task knowledge as tested at the end of the experiment was not affected by the SECPT (all $F_{(1,44)} < 1$, all $p > .30$, all $\eta^2 \leq 0.02$). On average, participants scored 3.95 points ($\pm 0.35 SEM$) in the test for the action–outcome associations and 7.69 points ($\pm 0.24 SEM$) in the test on stimulus–outcome associations and stimulus positions. Men

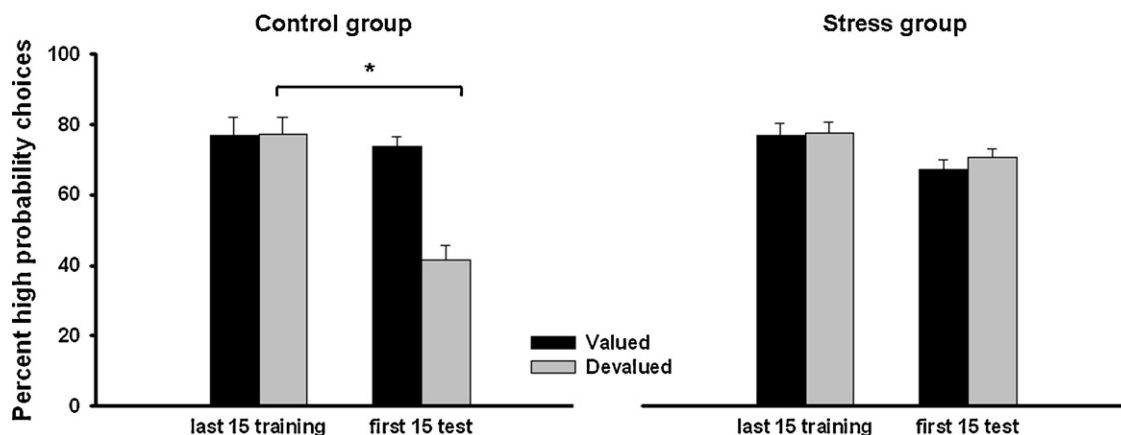


Figure 6 Percent high probability actions of controls and stressed participants in the last 15-trial block of training and the first 15-trial block of extinction testing. After selective outcome devaluation, controls showed a decrease in the choice of the high probability action associated with the food eaten to satiety ($* p < .01$) whereas the choice behavior of stressed participants was insensitive to the changes in outcome value. Data represent $M \pm SEM$.

and women performed similar in these tests (all $F_{(1,44)} < 2.3$, all $p > .14$, all $\eta^2 < 0.05$).

Discussion

Here, we studied the impact of acute SECPT stress after learning on goal-directed and habitual instrumental performance. SECPT stress administered before extinction testing rendered subjects' instrumental actions insensitive to changes in the value of the action goal and stress-induced cortisol elevations were associated with the selection of devalued instrumental actions. That is, acute SECPT stress impaired the goal-directedness of behavior and promoted habitual performance. Interestingly, this effect on instrumental behavior came without changes in explicit memory for action–outcome associations.

As participants were exposed to the SECPT after training and devaluation, SECPT effects on task acquisition and outcome devaluation cannot explain our findings. We assume that the SECPT-induced increase in habitual performance is at least partly owing to detrimental effects of the SECPT on cognitive control, in particular response inhibition. Cognitive control enables us to initiate, coordinate and update behavior (Miller, 2000). Critical to successful cognitive control is our ability to suppress actions that are no longer relevant or required (i.e. response inhibition). Interestingly, treatment with the stress hormone cortisol reduced monkeys' capacity to inhibit a specific goal-directed response (Lyons et al., 2000). Similarly, acute stress impaired performance in a “go/no-go” task that required subjects to respond to one stimulus but not to another (Scholz et al., 2009).

Recent fMRI studies indicate that goal-directed and habit performance rely in the employed devaluation paradigm on the prefrontal cortex (PCF) and the dorsolateral striatum, respectively (Valentin et al., 2007; Tricomi et al., 2009). Thus, acute stress might have impaired the functioning of the PFC, enhanced the functioning of the dorsolateral striatum, or both. The PFC exhibits a remarkably high density of glucocorticoid and mineralocorticoid receptors, the two receptors that mediate cortisol effects in the brain, and PFC-dependent behavior is highly stress sensitive (McEwen et al., 1986; Roozendaal et al., 2004). In contrast, glucocorticoid and mineralocorticoid receptors are expressed at relatively low levels in the striatum (McEwen et al., 1986) and striatum-dependent behavior appears to be rather insensitive to the influence of stress and stress hormones (Schwabe et al., 2009b). Given the differential stress sensitivity of the neural systems underlying goal-directed and habitual action, we suggest that the exposure to the SECPT impaired the goal-directed system and thus modulated the competition between the two systems (Yin and Knowlton, 2006) in favor of the habit system and at the expense of the goal-directed system. This view is in line with our assumption that the SECPT affected primarily participants' ability to inhibit learned responses since the PFC is also of central importance for cognitive control and response inhibition (Aron et al., 2004; Li et al., 2006). Further support for our view that acute stress led to impaired PFC functioning comes from a very recent study showing that chronic stress biases instrumental action towards habit (Dias-Ferreira et al., 2009). In this study, the chronic stress-induced switch towards more habitual

performance was accompanied by atrophy in the PFC and the associative dorsomedial striatum but hypertrophy in the dorsolateral striatum.

Although the present findings resemble our previous results (Schwabe and Wolf, 2009) suggesting that SECPT stress affects instrumental behavior primarily via processes involved in performance rather than acquisition, three differences between our previous and the present findings need to be pointed out. First, in our previous study stressed participants still favored the devalued instrumental action in the third extinction test block (i.e. after 45 trials) whereas the SECPT affected here mainly the choice behavior in the first extinction test block. Second, in our previous study the stress-induced increase in habit performance was paralleled by a decrease in explicit memory for action–outcome associations while SECPT stressed participants performed in the present study fairly well in the explicit memory test, same as controls. Third, in our previous study there were more “non-learners”, i.e. subjects that did not learn the instrumental responses, in the stress than in the control group whereas learning could not be affected by the SECPT here. These differences indicate that the switch from goal-directed to habit behavior was much more pronounced when participants were stressed before learning. This raises some doubts about whether the effect of stress on habit and goal-directed action can be attributed solely to effects on performance. It is tempting to speculate that stress before learning interferes with the formation of goal-directed actions whereas stress before testing impairs primarily cognitive control processes, such as response inhibition, which are required for a flexible adaptation of behavior to environmental changes. Unfortunately, effects of stress on the acquisition of instrumental actions can hardly be isolated because an extinction test after outcome devaluation is required to assess goal-directed vs. habitual action. If this test is given immediately after learning and devaluation (as in Schwabe and Wolf, 2009) then stress effects on acquisition cannot be separated from effects on performance. If devaluation and testing take place a longer time after learning then acquisition effects cannot be disentangled from consolidation effects. Future studies might solve this dilemma by using fMRI to examine stress-induced changes in PFC and dorsolateral striatum activity across learning. Rodent studies could also use neurochemical markers of activation (e.g. the release of acetylcholine; see Chang and Gold, 2003) to assess the contributions of these systems to instrumental learning.

Most studies on stress, learning and memory focus on quantitative performance parameters, such as a stress-induced increase or decrease in the number of items that are remembered (Kuhlmann et al., 2005; Buchanan et al., 2006; Payne et al., 2007). However, evidence is accumulating that stress affects not only the quantity of learning and memory, i.e. how much individuals learn and remember, but also the quality of learning and memory, i.e. what they learn and remember (for a review see Schwabe et al., in press-b). In particular, it has been shown that stress and glucocorticoids modulate learning strategies used in spatial navigation in favor of caudate nucleus-dependent stimulus–response (“habit”) memory and at the expense of hippocampus-dependent spatial (“cognitive”) memory (Kim et al., 2001; Schwabe et al., 2007, in press-a). Together with our previous findings (Schwabe and Wolf, 2009), the present data

show that this modulatory effect of stress is not specific to the domain of spatial navigation.

Given that we used food rewards in the present instrumental learning paradigm, the relation of stress and eating behavior needs to be addressed. Stress, the glucocorticoid stress hormones and eating behavior affect each other. Restraint eating may operate as a stressor and lead to increased salivary cortisol concentrations (Anderson et al., 2002). On the other hand, stress and stress-induced cortisol lead to overeating (for a review see Greeno and Wing, 1994). This might be explained by a disruptive effect of stress on self-control and willpower (Baumeister et al., 2007). Coping with stress (an act of self-control) may deplete large amounts of glucose which impairs subsequent self-control and increases glucose intake to refuel energy stores (Gailliot and Baumeister, 2007). In addition, stress might enhance food intake for reasons of emotion regulation, i.e. stressed individuals may indulge impulses to eat to make themselves feel better (Tice et al., 2001). This argument is in line with the stress-induced disruption of cognitive control suggested above.

Although the uncontrolled food consumption after stress can be viewed as a kind of habit behavior, we do not think that stress-related changes in hunger and eating can explain our findings. First, SECPT stressed participants did not indicate that they were hungrier or that they found the foods more pleasant than controls. Second and more importantly, the effects of stress on eating behavior appear to be biphasic. While an enhanced food intake can be observed hours after the stress exposure, the immediate stress effect is in the opposite direction. Corticotrophin releasing hormone (CRH) is known to have anorectic effects and restraint stress leads in rats to an acute reduction in food intake (Kaye et al., 1987; Krahn et al., 1990). Thus, we doubt that SECPT stressed participants performed the devalued instrumental action more often because they were hungrier at the extinction test, 25 min after the stressor. We rather argue that the SECPT has disrupted the system mediating cognitive control and goal-directed behavior and thus biased behavior towards more habitual action.

Here, we obtained a significant correlation between SECPT-induced cortisol and habit behavior. Although, this correlation does not imply any causality, it is in line with previous studies showing that corticosteroids play an important role in the stress-induced switch between memory systems (Schwabe et al., 2009a, in press-a). In addition to cortisol, however, there are a number of other neurotransmitters and hormones that are released in response to stress and may have affected instrumental action, including e.g. catecholamines, testosterone, and progesterone. Future studies could take blood samples or manipulate hormone and neurotransmitter levels pharmacologically to examine the role of some of these substances, including e.g. glucose which might be of particular interest in the paradigm used in this study.

Beyond these physiological changes, the exposure to the SECPT was most likely accompanied by a number of psychological changes. The SECPT has changed the emotional state of the participants and most likely increased their cognitive load. Thus, the SECPT may have operated as a distractor diverting participants' attention from the learning task (Wilson et al., 2009). Future studies should take such pos-

sible distraction effects into account and include more measures of the emotional and cognitive effects of the SECPT.

To conclude, we show that an acute exposure to the SECPT before extinction testing has a strong impact on whether instrumental performance is controlled by goal-directed or habit processes. Our findings indicate that behavior can become governed by habits after acute SECPT stress. These findings may be highly relevant for our understanding of relapse to drug addiction or other kinds of compulsory behavior.

Contributors

Lars Schwabe is the lead author. He contributed to the design of the study, analyzed the data and wrote the manuscript. Oliver Wolf contributed to the design of the study. Both authors contributed to and have approved the final version of the manuscript.

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Conflict of interest

Both authors report no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.psyneuen.2009.12.010](https://doi.org/10.1016/j.psyneuen.2009.12.010).

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