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Effects of psychosocial stress on the goal-directed and habit memory systems during learning and later execution.

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**Highlights**

- Exposure to psychosocial stress influences habitual performance.
- Goal-directed but not habit memory is affected by psychosocial stress
- Habit performance under stress comes from an impaired goal-directed capacity
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Abstract

Instrumental learning occurs through both goal-directed and habit memory systems, which are supported by anatomically distinct brain systems. Interestingly, stress may promote habits at the expense of goal-directed performance, since stress before training in an instrumental task was found to cause individuals to carry on with the learned association in spite of a devalued outcome. These findings nevertheless left pending questions, and it has been difficult to determine which system is primarily affected by stress (an improved habit system, an impaired goal-directed system, or both) and at what point the stress acts (at the moment of learning by making more resistant habits, or after devaluation by making individuals less sensitive to change in the outcome value). The present study (N=72 participants, 63 males and 9 females) aimed to answer these questions with (i) an instrumental task that dissociates the two memory systems and (ii) three conditions of psychosocial stress exposure (Trier Social Stress Test): stress induced before learning, before devaluation, and not induced for the control group. The study confirms that exposure to psychosocial stress leads to habitual performance. Moreover, it provides new insight into this effect by locating its origin as an impairment in the capacity of the goal-directed system rather than a reinforcement in habit learning. These results are discussed in light of recent neurobiological models of stress and memory.

Keywords: stress, habits, memory, instrumental learning.

1. Introduction

Many systems process information simultaneously and in parallel to build memory (Eichenbaum & Cohen, 2004; Gabrieli, 1998; White & McDonald, 2002). Regardless of the
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type of research paradigm, a distinction is usually made between a mainly cortex-based system that supports the acquisition of flexible declarative knowledge and a striatum-based system that builds rigid procedural knowledge of the link between a stimulus and a response (S-R), also known as a habit (Knowlton et al., 1996; Poldrack et al., 2001; Squire, 1992). For example, studies on the navigation strategies of subjects learning to move through a space (e.g., Iaria et al., 2003) or adapting to changes in landmarks (e.g., Packard & McGaugh, 1996) have distinguished a hippocampus-dependent spatial memory system that creates a cognitive map from a dorsal striatum-dependent habit memory system. The distinction between a cognitive memory system and a habit memory system has also been shown in the context of instrumental tasks, where subjects learn to produce specific responses through reinforcement. In this domain, learning occurs through a goal-directed system mainly based in the prefrontal cortex and a striatum-based habit system (Balleine & Dickinson, 1998; Corbit & Balleine, 2003; de Wit et al., 2009; Valentin, Dickinson, & O'Doherty, 2007; Yin & Knowlton, 2006). While the goal-directed system encodes the relationship between an action and the motivational value of the outcome, the habit system learns the association between a response and the preceding stimuli, with no reference to the outcome (Balleine & Dickinson, 1998). However, as learning proceeds through action that becomes increasingly more habitual, or stimulus-driven, the contribution of the goal-directed system decreases (Balleine & Dickinson, 1998). Once sufficient learning has taken place, the manipulation of the value of the outcome provides a unique opportunity to examine the engagement of the two systems. If the frequency of the action associated with a devalued outcome quickly decreases, this indicates that goal-directed behavior is favored over habitual behavior, but if the frequency of the action associated with a devaluated behavior fails to extinguish, then habitual responding prevails over goal-directed behavior.

1.1 Stress and Modulation of Goal-directed and Habit Memory Systems
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Research has shown that stress and the glucocorticoid hormones that are released in stressful contexts (mainly cortisol in humans) can cause a switch from the goal-directed to the habit system (Kim et al., 2001; Schwabe, Wolf, & Oitzl, 2010; Vogel et al., 2016). In a study using an instrumental task, Schwabe and Wolf (2009) demonstrated that participants who were stressed before learning with the socially evaluated cold pressure stress test (SECPT) (Schwabe, Haddad, & Schachinger, 2008) became less sensitive to outcome devaluation than control participants. Two distinct food rewards were used as reinforcement to train the participants to produce specific responses, but when one of these foods was later devalued by satiation, the stressed participants continued to display the learned response, while the control participants were quicker to show response extinction. The authors thus concluded that stress prompted habitual behaviors, but it was difficult to determine which system was primarily affected by stress manipulation. The resistance of a learned response to devaluation can be explained by an improvement in the habit system, an impairment in the goal-directed system, or a combination of both. For example, stressed individuals might create stronger habitual responses in the learning phase, which are more difficult to change after devaluation. While the effect of stress on memory is more established for declarative knowledge, recent studies in both animals (Ferragud et al., 2010; Quirarte et al., 2009) and humans (Guenzel, Schwabe, & Wolf, 2014) have also shown that stress can facilitate the consolidation of procedural striatum-based knowledge. Another possibility is that stress primarily affects the goal-directed system by perturbing the ability to evaluate the value of outcomes. Since the stresses in Schwabe and Wolf’s (2009) study were only induced once, both before learning, it was not possible to determine the origin of the stress effect. The authors therefore conducted another study with the same design but with the stress manipulation occurring after the learning phase, just before the devaluation procedure (Schwabe & Wolf, 2010b). They found a pattern similar to that of their earlier study, with more habitual responses for the devaluated outcome in the
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stressed as opposed to the non-stressed participants. They thus concluded that stress favors the expression of habitual behavior. However, the possible effect of stress on the formation of habits has still not been evaluated.

The present study was designed to test the reliability of the finding that stress prompts habitual performance; however, we isolated the effect on acquisition from the effect on performance and evaluated the specific influence of stress on each memory system. To examine reliability, we used the Trier Social Stress Test (TSST) to induce a psychosocial stress, with a potential monetary reward for an instrumental task. An adaptation of De Wit et al.’s (2009) task was chosen as it dissociates the contributions of the habit and goal-directed systems by having both standard control trials, in which the task can be learned by the two memory systems, and incongruent trials, in which the task can be learned only by the habit system because the response conflicts with the outcome (De Wit et al., 2009). To isolate the stress effects on learning and the stress effects on execution, the two phases of the task were carried out on two consecutive days. In a randomized, controlled between-subject design, the stress event occurred on the first day, before the learning phase, for the first group of participants (stress-on-day-1: SD1); on the second day, before devaluation, for the second group (SD2); and not at all for the control group (CTRL).

2. Method

2.1 Participants

A power analysis with an effect size of $f=0.38$ (derived from previous studies by Schwabe and Wolf, 2009; 2010b), a power level of 80%, and a p-value of .05 indicated that 72 participants were needed to find a significant effect with three independent groups at a specific time point. Accordingly, 72 students in a French university (9 females and 63 males; age range from 18 to 24 yr, $M=20.75 \pm 1.91$ yr) were recruited from a research methods class in exchange for course credits. All participants were free from medication and were
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nonsmokers. They had to refrain from eating and drinking caffeine or sweet beverages for the 3 hours preceding each session and to avoid intense physical exercise on the test days. Women taking oral contraceptives were excluded to avoid any effect on the neuroendocrine stress response (Kirschbaum et al., 1999). Participants received a monetary incentive on study completion based on their final score from the learning and devaluation phases (from 0 to 5 euros). The study was conducted in accordance with the Helsinki Declaration and was approved by the local ethics committee.

2.2 Design and Procedure

A minimization algorithm (Qminim, Saghaei & Saghaei, 2011) was used to randomize the participants into the three groups and balance the distribution of males and females between the experimental groups. Participants were randomly assigned to the SD1, SD2 or no-stress (CTRL) groups. The experiments were performed on two consecutive days in the afternoon between 1200h and 1800h, when cortisol levels are low and relatively stable (Kirschbaum et al., 1999). The experiment consisted of a training task on day 1 and a devaluation task on day 2. On day 1, participants were equipped with a HR monitor on arrival and the first saliva sample was collected. They then performed a 3-minute demonstration task followed by the stress induction or resting period, depending on the condition. Just before completing the learning task, a second saliva sample was collected and subjective stress and motivation for the task were assessed. On day 2, participants were again equipped with the HR monitor on arrival and the first saliva sample was collected. They then performed one block of control and incongruent trials to help them to recall the task (for 3 minutes) before the stress or resting period, depending on the condition. Just before completing the devaluation task, a second saliva sample was collected and subjective stress and motivation for the task were assessed. The protocol of the experiment is illustrated in Figure 1.

2.3 Instrumental task
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We adapted the instrumental task developed by De Wit et al. (2009) to dissociate the contributions of the cognitive and habit memory systems. All subjects were given a demonstration of the task after reading the following instructions: “In this game, you will have the chance to earn points by collecting items from inside a box on the screen. You open the box by pressing either the right or left key. If you press the correct key, the box will open to reveal a food item inside and points will be added to your total score. At the end of the study, your total amount of points will be converted into money (1 point equals 1 cent). However, if you press the incorrect key, the box will be empty and no points will be added to your total. Your task is to learn which key is the correct one. Sometimes it will be the left key and sometimes the right key. The picture on the front of the box should give you a clue about which is the correct response. To give you an idea about the game that you will be asked to play later on, we will run some demonstration trials. Just follow the instructions on the screen.”

After the demonstration, the participants were told that each box would remain on the screen for a fixed time and that they would gain no points if they failed to respond within this time. Only the first key press of each trial counted and the quicker a correct response was made, the more points were added to their total. Participants in each condition then had four practice trials. The total score was always displayed at the top of the screen. The outcomes were shown for 1 second. The inter-trial interval varied randomly between 0.5 and 2.5 seconds. Both accuracy and response time were recorded as the task outcomes. Response times faster than 200 ms were discarded.

The experimental design comprised two kinds of trials (de Wit et al., 2007): control and incongruent (see Figure 2). While performance in the control trials relied on both the goal-directed and habit systems, performance in the incongruent trials relied solely on the habit system. Two items were presented for both types of trial. Each item was presented eight
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times during each of the five blocks, amounting to a total of 160 trials for the learning phase. The control and incongruent trials were presented in randomized fashion in each block.

**Control:** Here, two foods were used as discriminative stimuli and two other foods were outcomes. For example, in one trial a picture of a banana signaled that pressing the right key would be rewarded with a pineapple, but left key presses would not be rewarded. In the other trial, a grape signaled that left key presses would be rewarded with a watermelon, but right key presses would not be rewarded. As noted, in the control discrimination, performance could be supported by both goal-directed and habit systems (see De Wit et al., 2007). We expected behavioral control through direct banana→and pineapple→left associations to build up concurrently in the habit system. However, with only limited training, the performance of the goal-directed system was expected to have predominant control.

**Cue-Outcome Incongruent:** For this type of trial, a goal-directed approach was expected to cause response conflict, as the stimulus-outcome pair was reversed across the trials. For example, a strawberry signaled that pressing the right key would be rewarded with an orange, whereas an orange signaled that pressing the left key would be rewarded with a strawberry. When strawberry acted as the discriminative stimulus, the correct right key press should have been activated via a strawberry→orange→right (S→O→R) associative chain, but because strawberry also functioned as an outcome for the opposite left key press, the latter incorrect response should have been activated directly via a strawberry→left (O→R) associative link. As a result, it was expected that it might be difficult, if not impossible, to solve the cue-outcome incongruent condition with the goal-directed system. Instead, we assumed that the participants would be forced to rely solely on the associations encoded in the habit system (see De Wit et al., 2007).

*2.4 Devaluation task*
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In our devaluation task, the participants were told that some of the answers would no longer earn points but would instead remove them (see devaluation panel of Figure 2). One item of each type of stimuli was devalued, while the other kept its value. Therefore, to avoid any loss of points in the devalued trials, the participants had to press the contrasted button associated with an empty box. For example, while using the left button for the banana stimulus would lead to a pineapple associated with points earned in the learning task, the same left button for the banana stimulus would again lead to the pineapple but points would be lost. Each item from the control and incongruent conditions was presented 12 times in each of the two blocks, for a total of 96 trials. Within a block, the selection of the trials was random. To keep the participants motivated, the monetary value of a point was double that of the learning session (1 point = 2 cents).

2.5 Psychosocial stress

Psychosocial stress was induced with an adapted version of the TSST (Hua et al., 2014). The participants had to prepare and give a job interview in front of an audience but did not have to perform the mental arithmetic task of the original TSST. As previously shown, this protocol causes significant sympathetic and endocrine activation (Schommer, Hellhammer, & Kirschbaum, 2003), which is used as a read-out of the experienced stress. During the initial briefing, participants were instructed about the task. They were given 5 minutes to prepare a presentation in which they would promote their candidacy for a fictional job tailored to their real-life interests and qualifications. They then stood in front of two senior professors of the university (one male and one female) and a video camera recording the session, and orally defended their candidacy. They were not informed of the exact interview duration. The interview ended after 5 minutes, but the jury asked standardized questions if they stopped speaking beforehand. In the control conditions, the participants stood in the room, with magazines but no audience or camera, for 10 minutes.
2.6 Subjective stress ratings

In line with the study of Schwabe and Wolf (2009), subjective stress was measured just after the job interview or the waiting period, depending on the condition. The participants were asked to rate how stressful, painful and unpleasant they found the interview or waiting period on a scale from 0 (“not at all”) to 100 (“very much”).

2.7 Subjective reports of motivation

After the stress induction or resting period, participants rated how motivated they were to pursue the tasks of the experimental session on a visual analog scale from 0 (“not at all”) to 100 (“very much”), as used by Schwabe and Wolf (2009).

2.8 Heart rate and heart rate variability

Heart rate (HR) was derived from a thoracic belt connected to a HR monitor (Polar RS800, Polartec Kempele, Finland). The mean heart rate (HR) and the root mean square of the successive differences of the interbeat interval (RMSSD), a common measure of heart rate variability adapted for short-term measurement (Malik, 1996), were calculated for the full four periods of the TSST procedure: baseline, preparation, interview and recovery.

2.9 Salivary cortisol

Saliva samples were collected on arrival at the lab and after the TSST or resting period (about 5 minutes after the end of the TSST) on day 1 and day 2 with a cotton Salivette (Sarstedt, Numbrecht, Germany), stored at room temperature until completion of the session, and then kept at -20°C until analysis. Free cortisol concentrations were measured using an immunoassay (Cortisol EIA kit, Oxford Biomedical Research, Rochester Hills, MI, USA). Inter- and intra-assay coefficients of variability were below 10%.

2.10 Data Analysis

All data were first checked for normality through visual inspection (frequency histograms and quantile-quantile plots of the residuals) and a Shapiro-Wilk test. All
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psychological and physiological variables assessing the stress response were analyzed by means of general linear models (GLM) for repeated measures and Fisher’s least significant difference post-hoc tests when needed. Concerning accuracy in the instrumental task, a specific approach was used to model the shape of the data. Given that the dependent variable of this task (i.e., number of errors per block) is a count variable with only positive integer values, we used generalized linear mixed models (GLMM) with a Poisson distribution and a log link (see Stroup, 2012). Repeated measures were taken into consideration by including a random intercept effect structured by the participants and types of trials to account for the non-dependency of the observations (Judd, Westfall, & Kenny 2012). Simple contrasts with least significant differences helped to interpret the direction of the effects when needed. All reported $p$-values are two-tailed.

3. Results

3.1 Subjective and physiological responses to stress

Subjective stress ratings, motivation ratings, heart rate, HRV, and salivary cortisol responses were used to evaluate the consequences of the psychosocial stress task. Table 1 presents the descriptive statistics for each of these variables. For the sake of clarity, descriptive statistics for transformed data are presented before transformation.

3.1.1 Subjective stress ratings

The distribution of this variable was negatively skewed due to the high number of low stress scores in the control sessions. An inverse transformation was thus applied. A GLM with the day of testing as the within-subject factor and group as the between-subject factor revealed a two-way interaction between these two factors $F(2, 72)=15.711$, $p=.0001$, $\eta^2=.304$. On the first day, SD1 participants reported higher stress ratings than those in the CTRL group and the SD2 group, $p=.001$ and $p=.023$, respectively. On the second day, SD2 participants
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reported higher stress ratings than those in the CTRL group and the SD1 group, \( p=.0001 \) and \( p=.0001 \), respectively. No other significant differences were found.

### 3.1.2 Subjective reports of motivation

Although participants reported higher stress ratings when they experienced the stress induction, it did not seem to affect their motivation for the instrumental task, as no main or interaction effects were found in the GLM, \( F(2, 72)<0.2 \).

### 3.1.3 Heart rate

A GLM with two within-subject factors (day of testing: day 1 vs. day 2; time of measurement: baseline, preparation, interview, recovery) and condition as a between-subject factor revealed a significant effect of the time of measurement \( [F(3, 67)=8.171, \ p=.0001, \ \eta^2=0.132] \), an interaction of time of measurement with group \( [F(6, 68)=5.633, \ p=.002, \ \eta^2=0.199] \), and an interaction of day of testing with group \( [F(2, 69)=7.423, \ p=.001, \ \eta^2=0.177] \). Crucially, a significant three-way interaction was observed \( [F(6, 68)=31.781, \ p=.0001, \ \eta^2=0.584] \). As shown in Table 1, on day 1 of the experiment, SD1 participants had higher heart rate values than the CTRL and SD2 groups during the preparation and interview periods \((ps<.05)\). On day 2 of the experiment, SD2 participants had higher heart rate values than the CTRL and SD1 groups but only during the time of the interview \((ps<.05)\).

### 3.1.4 Heart rate variability

A GLM with two within-subject factors (day of testing: day 1 vs. day 2; time of measurement: baseline, preparation, interview, recovery) and condition as a between-subject factor revealed a significant effect of time, \( [F(3, 67)=14.835, \ p=.0001, \ \eta^2=0.177] \), a day × condition interaction \( [F(2, 69)=4.670, \ p=.013, \ \eta^2=0.119] \), and a time × condition interaction \( [F(6, 67)=2.499, \ p=.023, \ \eta^2=0.068] \). Crucially, a significant three-way interaction was observed \( [F(6, 68)=31.781, \ p=.0001, \ \eta^2=0.584] \). On day 1 of the experiment, the only differences were found during the interview period. During this time, SD1 participants had a
lower RMSSD than CTRL participants. \( p=.025 \). On day 2, differences were found at baseline and during the interview. During the interview, SD2 participants had a lower RMSSD than participants in SD1 and CTRL \( p<.05 \).

3.1.5 Salivary cortisol

Salivary samples of eight participants were not included in the analysis due to an insufficient amount of saliva or food contamination. The GLM with two within-subject factors (day of testing: day 1 vs. day 2; time of measurement: before vs. after the psychosocial task) and condition as a between-subject factor revealed a three-way interaction \( [F(2, 63)=7.773, p=.007, \eta^2=.113] \). As expected, post-hoc tests indicated that the only significant increases occurring after the psychosocial task concerned SD1 participants on day 1 and SD2 participants on day 2, \( p=.013 \) and \( p=.0001 \), respectively.

3.2 Effects of stress on instrumental learning

Number of errors: The type of trial (control vs. incongruent), the block number (block 1 to block 5) and the conditions were entered as fixed factors in the GLMM. A main effect of the block number \( [F(4, 678)=104.408, p=.0001 \), indicating a lower number of errors in time] and a main effect of the type of trial \( [F(1, 678)=93.589, p=.0001 \), indicating a higher number of errors for incongruent than for control trials] were found. Importantly, the three-level interaction of block number × trials × condition was also significant, \( F(12, 678)=3.152, p=.001 \). For incongruent trials, no significant differences were found between conditions in any block. However, for control trials, SD1 participants made more errors in the first block than those in SD2 \( p=.007 \). The difference between the number of errors made by SD1 and CTRL participants approached the significance threshold \( p=.086 \). In the second block, more errors were still made in SD1 than SD2 \( p=.016 \). No differences between conditions were found in the later blocks. Figure 3 illustrates this pattern of results.
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Response time: The type of trial (control vs. incongruent), the block number (block 1 to block 5), the experimental conditions, and all possible interactions between these variables were entered as fixed factors in the GLM. A main effect of the block number \([F(4, 288)=40.623, p=.0001, \eta^2=.361\), indicating a linear decrease from the first block \((M=825ms, ES=16ms)\) to the fifth block \((M=683ms, ES=12ms)\)\] and a main effect of the type of trial \([F(1, 72)=17.809, p=.0001, \eta^2=.198\), indicating slower response time for incongruent \((M=745ms, ES=11ms)\) than for control trials \((M=720ms, ES=11ms)\)\] were found. No other effects were found.

3.3 Effects of stress on responses to devaluation

Number of errors: The type of trial (control vs. incongruent), the selective valuation (valued vs. devalued stimuli), the block number (block 1 vs. block 2) and the conditions were entered as fixed factors in the GLMM. None of the main or interaction effects involving the type of trial reached significance. However, the main effects of selective valuation \([F(1, 588)=17.548, p=.0001, \eta^2=.174\), indicating more errors for devalued than for valued trials], block \([F(1, 588)=82.593, p=.0001, \eta^2=.198\), indicating more errors in block 1 than in block 2], and condition \([F(2, 588)=4.341, p=.013, \eta^2=.018\), indicating fewer errors for SD1 than for CTRL and SD2] were found. A two-level interaction between condition and valuation was also found, \([F(2, 588)=6.217, p=.002\). While more errors were made in SD2 than SD1 and CTRL for devalued trials \((p=.013\) and \(p=.026\), respectively), fewer errors were made in SD1 than CTRL and SD2 for valued trials \((p=.001\) and \(p=.004\), respectively). In addition, the three-level interaction of condition \(\times\) valuation \(\times\) block was also significant \([F(2, 588)=7.150, p=.001\]. The pattern of the results is illustrated in Figure 4. For devalued trials, the contrast analysis indicated that in block 1, more errors were made in SD2 than SD1 \((p=.024\). The difference between the number of errors made by participants in SD2 and CTRL approached the significance threshold \((p=.085\). The pattern was similar in block 2, as more errors were made in SD2 than in SD1 \((p=.018)\). For
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valued trials, the contrast analysis indicated that in block 1, more errors were made in SD2 than SD1 but this difference did not reach significance ($p=.052$). No significant difference emerged in block 2.

**Response time:** The type of trial (control vs. incongruent), the block number (block 1 to block 5), the value (valued vs. devalued stimuli) and the conditions were entered as fixed factors in the GLM. A main effect of the block number \[F(1, 72)=54.612, \ p=.0001, \ \eta^2=.435,\] indicating faster response time in the first ($M=847ms, ES=19ms$) than in the second block ($M=737ms, ES=15ms$)] and a main effect of the value \[F(1, 72)=69.099, \ p=.0001, \ \eta^2=.493\] indicating slower response time for devalued ($M=874ms, ES=22ms$) than for valued stimuli ($M=710ms, ES=13ms$)] were found.

4. Discussion

This study examined the impact of psychosocial stress (TSST) on the goal-directed and habit memory systems during both the learning and post-devaluation execution of a task. We used an instrumental task that dissociates the two memory systems. Performance of the control discrimination trials relied on both systems, whereas performance of the incongruent discrimination trials was supported solely by the habit system. The results suggested that the TSST administered before devaluation made participants less sensitive to changes in the outcome. In contrast to non-stressed control participants, participants exposed to stress on day 2 (before devaluation) continued to perform the action associated with monetary gain after this outcome had been devalued. Moreover, stress before learning seemed to result in slower learning of goal-directed behavior but better retention of habits.

Our results tended to replicate the two studies by Schwabe and Wolf (2009; 2010b), showing that stress before devaluation yielded habitual behavior. In their first study, these authors showed that a socially evaluated cold pressure test (SECPT) before learning rendered participants insensitive to change in the value of the outcome. Their second study helped to
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localize the effect, as they demonstrated that stress (SECPT) before devaluation rendered behavior habitual, whereas learning performance was obviously unaffected. Although our findings resemble those of Schwabe and Wolf (2009), suggesting that stress affects instrumental behavior primarily via processes involved in performance rather than acquisition, some of the differences between their studies and ours should be noted.

First, our study had two experimental groups plus a non-stressed control group, and the experimental group participants were either exposed to a stress before learning on day 1 or before devaluation on day 2. Our study therefore informs on the effects of stress on learning. In contrast to the findings of Schwabe and Wolf (2009), our results suggested that stress before learning (SD1 group) impaired the performance of control trials in comparison with no stress (CTRL and SD2, which was similar to CTRL at this point). This effect indicates that stress influenced goal-directed learning negatively, as performance on the incongruent trials was unaffected. Nevertheless, the negative effect of stress on the control trial performance was only localized to the first blocks. This result suggests either that the effect of stress on goal-directed learning was short-lasting and quickly dissipated, or that the goal-directed system was no longer needed in the later blocks of the task, as performance is known to typically shift from the goal-directed to the habit system through repetition (Balleine & Dickinson, 1998; Graybiel 2008). Stress may have impeded deliberative control (Wood & Runger, 2015). In sum, stress seems to have impaired the goal-directed system during both learning and performance after devaluation. It is important to note that these effects could not be explained as a speed–accuracy trade-off because the experimental condition had no effect on response time in the instrumental task on the first and second days.

In addition, participants who received the stress manipulation on day 1 performed better on day 2, particularly on the valued trials. Even though there was no effect on performance at the end of learning (suggesting no effect on encoding), it is possible that stress
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helped the participants to construct more durable knowledge (suggesting a positive effect on consolidation). While some of the effects of stress on memory consolidation have been amply demonstrated (e.g., Buchanan & Lovallo, 2001), these effects have been more rarely shown for habit memory. Recent findings from spatial memory studies nevertheless suggest that stress hormones have a positive effect on habit consolidation. For example, following an infusion of corticosterone into rat striatum, Quirarte et al. (2009) reported the enhanced consolidation of stimulus-response (S-R) associations on a test conducted 48 hours later. Similarly, Guenzel, Wolf, and Schwabe (2014) found that while hydrocortisone injection in humans did not affect learning S-R associations in a spatial environment, it led to better retention in a recollection test conducted a week later. Nevertheless, we do not think this stress-induced effect on consolidation is likely to explain the difference in task performance after devaluation. Indeed, the participants who received the stress before devaluation still selected the responses that led to the devaluated outcomes more often than the participants of the control group who had never been exposed to the stress.

Several fMRI studies during instrumental tasks have shown that goal-directed actions are mediated by the medial prefrontal cortex (PFC) and that habit performance is mediated by the dorsolateral striatum (Tricomi et al., 2009; Valentin et al., 2007). It therefore seems that stress impaired PFC functioning. Along these lines, an fMRI study in humans showed that stress increased habitual behavior primarily because of an impairment of PFC-cognitive control mechanisms (Ossewaarde et al., 2011). Specifically, stress decreased the reward-related responses in the medial PFC without affecting striatal responses. This effect may be explained by the high density of glucocorticoid and mineralocorticoid receptors in the PFC (McEwen et al., 1986). These two receptors mediate cortisol effects in brain areas like the PFC as they bind to circulating cortisol, a hormone that easily crosses the blood–brain barrier. For this reason, it has been suggested that the PFC is particularly sensitive to stress (Arnsten,
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2009; Roozendaal et al., 2004). Stress also activates other pathways, such as the catecholamine system, and more particularly the noradrenaline pathway. Stress typically stimulates the noradrenaline pathway by provoking a large augmentation from the baseline values (Arnsten, 2009). It is interesting to note that high activation of the noradrenaline pathway has also been shown to impair PFC-dependent functions (Brennan & Arnsten, 2008). This interpretation has been supported by the administration of beta-adrenoceptor antagonist before stress (Schwabe et al., 2010a, 2011) and the neuroimaging data of Schwabe et al. (2012), which showed that glucocorticoids and noradrenaline interact to decrease activity specifically in the brain structures that underlie goal-directed action in instrumental learning (i.e., orbitofrontal and medial prefrontal cortex).

Exposure to the TSST was accompanied by a number of psychological changes. A study by Scholz et al. (2009) demonstrated that acute stress induces emotional reactions like heightened anxiety and irritability, which may occur independently of sympathetic or HPA axis responses. By changing the participants’ emotional state, the TSST may have increased their cognitive load by modulating the interaction between “higher executive” and “lower emotional” processes (Luethi, Meier, & Sandi, 2007; Schwabe & Wolf, 2009; van Marle et al., 2009). Brain activation during emotional distraction was found to be enhanced in ventral affective areas, while dorsal executive areas tended to show less deactivation after stress (Oei et al., 2012). Stress increased the sensitivity of the amygdala and inferior temporal activity (van Marle et al., 2009) and reduced dorsal prefrontal activation during working memory (Qin et al., 2011). These results suggest that acute stress may have shifted participants’ attention from the learning task (Oei et al., 2012). Future studies should take such possible distraction effects into account and include more measures of the emotional and cognitive effects of the TSST.
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Our study also differed from previous studies by manipulating stress in a more ecological way: psychosocial stress was manipulated by having the participants defend their work qualifications to two university professors. Based on the results, we might conclude that psychosocial stress has the same effect as physiological stress, given that our adapted version of the TSST had effects similar to those of previous studies that used prolonged immersion in cold water (Schwabe & Wolf, 2009; 2010b). This study therefore extends the findings on the effects of stress on habits to include the effects of psychosocial stress, which adds ecological validity as this type of stress is experienced in a wide range of social contexts (e.g., work, exams, evaluations, public speaking, or media interviews). Although the TSST remains a laboratory manipulation, we believe that our findings extend the generalizability of the negative effects of stress to the process of integrating a change in the value of real-life actions.

Some limitations should be mentioned. First, the stress effects that we observed cannot be generalized to the general population, since our sample was young and mostly male. In addition, no information was collected on the menstrual cycle of the women, although this variable should have been controlled as endogenous cortisol concentrations tend to vary across the cycle (Nepomnaschy et al., 2011). Another limitation concerns the transfer of this paradigm to real life: although we have used the word habit, it can be argued that we examined habit-like behavior rather than real behavioral habits in our study.

To conclude, the present study confirms that exposure to stress leads to habitual performance. However, our findings provide a better understanding of this effect by locating its origin as an impairment in the capacity of the goal-directed system rather than a reinforcement in habit learning. These results provide insight into why we behave in an automatic way after a stress and, more specifically, why there is sometimes a gap between our intended behavior and our actual behavior, the latter often reflecting an old and firmly entrenched behavioral response (Ouellette & Wood, 1998). Such stress effects could thus be
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particularly relevant for explaining the execution of no-longer wanted behaviors such as smoking, eating disorders and, more generally, any addictive behavior.

Role of the founding source

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Acknowledgement

This work was funded by a CIFRE scholarship. We thank Lars Schwabe for his help on the experiment.
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Figure 1. Timeline of the experiment.

Notes: CTRL = participants of the control group that received no stress induction on either day of the experiment. SD1 = participants of the group receiving the stress induction on day 1. SD2 = participants of the group receiving the stress induction on day 2.
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Figure 2: Illustrative examples of the congruent and incongruent trials in the learning phase of the instrumental task and the devaluation, and illustrative example of a congruent trial.

Notes: RR= right response, LF= left response
LEARNING SESSION

Figure 3. Percentage of correct responses made in the instrumental task on day 1 as a function of the type of trial (panel A represents incongruent trials and panel B represents control trials) and the group of participants.

Notes: CTRL = participants of the control group that received no stress induction on either day of the experiment. SD1 = participants of the group receiving the stress induction on day 1. SD2 = participants of the group receiving the stress induction on day 2.
Figure 4. Percentage of correct responses made in the instrumental task on day 2 as a function of the selective devaluation (panel A represents valued trials and panel B represents devalued trials) and the group of participants.

Notes: CTRL = participants of the control group that received no stress induction on either day of the experiment. SD1 = participants of the group receiving the stress induction on day 1. SD2 = participants of the group receiving the stress induction on day 2.
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Table 1: Descriptive Statistics for Variables Assessing the Consequences of the Psychosocial Stress Task

<table>
<thead>
<tr>
<th></th>
<th>First day</th>
<th>Second day</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CTRL</td>
<td>SD1</td>
</tr>
<tr>
<td>Subjective ratings of stress</td>
<td>12.4±14.00</td>
<td>68.8±10.15</td>
</tr>
<tr>
<td>Subjective motivation</td>
<td>58.72±19.81</td>
<td>56.40±19.06</td>
</tr>
<tr>
<td>Variability RMSSD (ms)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Baseline</td>
<td>53.85±27.80</td>
<td>55.93±36.08</td>
</tr>
<tr>
<td>- Preparation</td>
<td>53.31±26.21</td>
<td>50.19±38.86</td>
</tr>
<tr>
<td>- Interview</td>
<td>53.63±21.77</td>
<td>38.95±25.49</td>
</tr>
<tr>
<td>- Recovery</td>
<td>66.35±25.36</td>
<td>56.80±31.67</td>
</tr>
<tr>
<td>Heart rate (bpm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Baseline</td>
<td>76.15±12.34</td>
<td>78.34±15.32</td>
</tr>
<tr>
<td>- Preparation</td>
<td>76.20±15.41</td>
<td>86.61±18.62</td>
</tr>
<tr>
<td>- Interview</td>
<td>78.12±18.40</td>
<td>94.78±18.47</td>
</tr>
<tr>
<td>- Recovery</td>
<td>82.38±27.19</td>
<td>77.69±13.81</td>
</tr>
<tr>
<td>Salivary cortisol (nmol/l)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes. Means are presented ± standard deviations. N=75 for all variables but salivary cortisol measurements (N=66). CTRL= participants of the control group that received no stress induction on either day of the experiment. SD1= participants of the group receiving the stress induction on day 1. SD2= participants of the group receiving the stress induction on day 2. TSST= Trier Social Stress Test