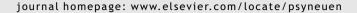


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Socially evaluated cold pressor stress after instrumental learning favors habits over goal-directed action

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KEYWORDS

Stress; Cortisol; Instrumental learning; Goal-directed action; Habits 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

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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 (Roozendaal 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, SECPT) 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.

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