



SHORT COMMUNICATION

Stress disrupts response memory retrieval

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Summary Stress effects on memory are well-known. Most studies, however, focused on the impact of stress on hippocampus-dependent ‘declarative’ memory processes. Less is known about whether stress influences also striatum-based memory processes, such as stimulus–response (S–R) memory. First evidence from rodent experiments shows that glucocorticoid stress hormones may enhance the consolidation of S–R memories. Whether stress affects also S–R memory retrieval remains largely elusive. Therefore, we tested in the present experiment in humans the effect of stress on the retrieval of S–R memories. Healthy men and women were trained to locate three objects in an S–R version of a virtual eight-arm radial maze. One week later, participants underwent a stressor or a control condition before their memory of the S–R task was tested. Our results showed that participants ($n = 43$) who were exposed to the stressor before retention testing made significantly more errors in this test trial, suggesting that stress impaired S–R memory retrieval. Moreover, high cortisol concentrations were associated with reduced S–R memory. These findings indicate that stress may affect memory retrieval processes in humans beyond hippocampal ‘declarative’ memory.

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1. Introduction

Stressful experiences trigger a cascade of physiological changes, including the release of glucocorticoids and catecholamines. These stress mediators may modulate cognitive processes. Particularly, stress (hormone) effects on hippocampus-dependent ‘declarative’ learning and memory are well documented (Roosendaal et al., 2009; Schwabe et al., 2012). These effects may depend on the intensity of the

stressor (Taverniers et al., 2010). Moreover, it is generally assumed that these stress effects are time-dependent, and that stress enhances the consolidation but impairs the retrieval of ‘declarative’ memories (De Quervain et al., 1998; Smeets et al., 2008; Roosendaal et al., 2009).

Whether and how, stress affects memory processes beyond hippocampus-dependent ‘declarative’ memory remains largely elusive. For decades, the predominant view held that stress has a specific and particularly strong influence on the hippocampus (Lupien and Lepage, 2001). There is, however, by now accumulating evidence that stress may also alter non-hippocampal, in particular striatal memory processes (Schwabe et al., 2010b). For example, recent rodent studies demonstrated that glucocorticoid injections

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into the dorsal striatum directly after learning of a stimulus–response (S–R) or inhibitory avoidance task enhanced the consolidation of these tasks (Medina et al., 2007; Quirarte et al., 2009; Sánchez-Resendis et al., 2012). Whether stress may also alter the retrieval of consolidated S–R memories and whether stress affects S–R memories in humans remains largely elusive.

Therefore, our study examined the influence of stress on the retrieval of S–R memories in humans. Healthy participants were trained in an S–R navigation task in a virtual environment. Previous fMRI studies that used a very similar task demonstrated that such S–R navigation memory depends on the striatum and not on the hippocampus (Iaria et al., 2003; Bohbot et al., 2007). One week after training in the S–R task, participants underwent a stressor or a non-stressful control task before S–R memory was tested. Because stress hormones enhanced the consolidation of S–R memories (Quirarte et al., 2009) in a similar manner as the consolidation of declarative memories, we expected that stress effects on S–R memory retrieval would also resemble those on declarative memory retrieval, i.e., we predicted that stress would impair the retrieval of S–R memories.

2. Materials and methods

2.1. Participants

Sixty healthy, non-smoking students (30 men, 30 women; age: $M = 23.88$ years, $SEM = .34$ years; body-mass-index: $M = 22.73$ kg/m², $SEM = .30$ kg/m²) without a history of any neurological or psychiatric diseases, drug abuse or medication intake provided written informed consent for their participation in this study. We tested only women that were not taking hormonal contraceptives and women were not tested during their menses.

2.2. Procedure

Participants were tested in a between-subject design on two experimental days with an interval of one week: day 1, learning; day 2, stress (or control condition) and retention testing. In order to control for diurnal variations of cortisol, all testing took place in the afternoon between 13:00 and 18:00 h.

After participants' arrival at the laboratory on day 1, blood pressure measurements were taken and a single saliva sample was collected (see below). Before the training in the S–R learning task, participants completed two practice trials, in order to become familiar with navigating in a virtual environment. In these practice trials, participants were instructed to collect four objects in a computer-based 3D virtual room. All objects were inserted into wooden hollows and could be collected by using the left-, right- and forward-arrow keys. Afterwards, training in the S–R task started. In this task, participants were presented a 3D virtual 8-arm radial maze on a computer screen (Fig. 1A). Both, the computer-based virtual room for practice and the computer-based radial maze for S–R learning, were designed using a commercially available video game editor (Gamestudio, Conitec, Germany).

We designed the radial maze task to parallel the key features of radial maze tasks that have been used in rodents to examine S–R memory (McDonald and White, 1993). The radial maze consisted of eight identical arms originating from a center platform. Each maze-arm was surrounded by high walls and contained a wooden hollow at the end. Different objects (book, cake, and bag) were placed in three of these hollows and participants were instructed to collect these objects in a given order (book, cake, bag) as quickly as possible. The location of the objects was constant in all trials. Three learning trials were given, each with a maximum duration of 3 min. If participants made one or more errors in the last trial, up to three extra trials were given. The time to complete a trial and the errors per trial were (automatically) recorded for statistical analysis. Importantly, the eight maze arms looked exactly the same and no extra-maze cues were provided. There was just a single intra-maze cue (a chair) that could be used for orientation. Thus, participants could learn the location of the objects solely by linking the single intra-maze cue with a sequence of movements. Previous neuroimaging studies that used a very similar task design demonstrated that such "response" learning is dependent on the caudate nucleus (Iaria et al., 2003; Bohbot et al., 2007). Participants were not informed that memory for the S–R task would be tested on the second day.

On the second day, seven days after experimental day 1, participants were randomly assigned to the stress or control condition. Participants in the stress condition were exposed to the socially evaluated cold pressor test (SECPT), as described in detail elsewhere (Schwabe et al., 2008). Briefly, participants immersed their right hand up to and including the wrist for as long as possible (maximum 3 min) into ice water (0–2°). They were videotaped and observed by a non-reinforcing, unsociable experimenter. In the control condition, participants immersed their right hand up to and including the wrist for 3 min into warm water (35–37°). They were neither videotaped nor monitored by the experimenter.

In order to verify the successful stress induction by the SECPT, subjective and physiological measurements were taken at several time points before and after the stress and control condition, respectively. Immediately after the SECPT/control condition, participants rated on a scale from 0 ("not at all") to 100 ("very") how unpleasant, stressful and painful they had experienced the stress/control condition. Moreover, we collected saliva samples immediately before the stress/control condition (baseline), 20 min after the SECPT/control condition, i.e., immediately before the retention test, as well as 40 min after the SECPT/control condition. Saliva samples were collected with Salivette collection devices (Sarstedt, Nümbrecht, Germany) and stored at about –20°. The free fraction of the stress hormone cortisol was analyzed from saliva by means of an immunoassay (IBL, Hamburg). Interassay and intra-assay coefficients of variance were below 10%. Furthermore, we measured blood pressure with the Dinamap system (Critikon, FL) shortly before, during and, shortly after the stress/control condition.

After a 25 min-break during which subjects were allowed to read, retrieval of S–R memory was tested. Participants completed another trial of the S–R task. The radial maze was exactly the same as during training on day 1. Again, participants were instructed to collect the three objects as quickly as possible and in the same order as on day 1.

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