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Remembering under stress: Different roles of autonomic arousal and glucocorticoids in memory retrieval

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Abstract It is commonly assumed that stress impairs memory retrieval. Glucocorticoids, released with a delay of several minutes in response to stressful experiences, are thought to play a key role in the stress-induced retrieval impairment. Accordingly, most studies on the impact of stress on retrieval tested memory a considerable time after stressor exposure, when glucocorticoid levels were elevated. Here, we asked how stress affects memory when retrieval takes place under stress, that is, when stress is part of the retrieval situation and glucocorticoids are not yet increased at the time of testing. To contrast stress effects on ongoing and delayed memory retrieval, 72 participants learned first neutral and emotional material. Twenty-four hours later, half of the learned material was tested either in a stressful, oral examination-like testing situation or in a standard, non-stressful free recall test. Memory for the other half of the learned material was assessed 25 min after the first, stressful or non-stressful retention test. Significant increases in blood pressure and salivary cortisol confirmed the stress induction by the first, examination-like testing situation. Retrieval performance under stress was positively correlated with the blood pressure response to the stressor but unaffected by cortisol. Conversely, retrieval performance 25 min post stress was negatively correlated with the cortisol response to the stressor, particularly for emotional items. These results suggest that the same stressor may have opposite effects on ongoing and delayed memory retrieval, depending on the presence of autonomic arousal and glucocorticoids.

1. Introduction

When we perceive an actual or potential threat to our well-being (i.e., a stressor), our body initiates a cascade of physiological events. Within seconds after stressor exposure,

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the autonomic nervous system triggers the release of adrenaline and noradrenaline from the adrenal medulla, which in turn stimulate noradrenergic nuclei in the brain by activating vagal afferents to the nucleus of the solitary tract. In parallel to the activation of the autonomic nervous system, the hypothalamus-pituitary-adrenal axis leads via intermediate steps and with a delay of several minutes to the secretion of glucocorticoids (cortisol in humans) from the adrenal cortex. In concert with numerous other hormones, peptides, and neurotransmitters that are released during stressful experiences, adrenaline, noradrenaline, and glucocorticoids help us cope with ongoing challenges and, at the same time, prepare us for similar situations in the future. An integral part of how these stress mediators prepare us for future stress situations is by shaping learning and memory processes (Diamond et al., 2007; Joëls et al., 2011; Schwabe et al., 2012). Stress hormones promote lasting memories; in particular the formation of memories for events that are related to the stressor is enhanced by stress hormones (Cahill et al., 2003; McGaugh and Roozendaal, 2002; Sandi et al., 1997; Smeets et al., 2007; Zoladz et al., 2011).

Although stress may facilitate memory formation and consolidation, it is commonly assumed that stress impairs memory retrieval (de Quervain et al., 1998; Guenzel et al., 2013; Kuhlmann et al., 2005; Roozendaal et al., 2004; Schwabe and Wolf, 2009; Smeets et al., 2008; but see also Schilling et al., 2013; Schwabe et al., 2009). These disruptive effects of stress on retrieval are mainly mediated by glucocorticoids (Buchanan et al., 2006; de Quervain et al., 1998, 2000), in interaction with noradrenergic arousal (de Quervain et al., 2007; Roozendaal et al., 2004, 2006a). The stress-induced impairment of memory retrieval might be beneficial for coping with stress in the sense that it reduces distraction by stressor-unrelated information and allows well-established habits and routines to control behavior (Schwabe and Wolf, 2010, 2013).

A general retrieval impairment in stressful situations, both for stressor-related and stressor-unrelated information, however, would be clearly disadvantageous. According to a popular model (Joëls et al., 2006), rapid noradrenaline and glucocorticoid actions facilitate specifically the processing of information relevant to the ongoing stressor. Although this model focusses primarily on memory formation, there is some evidence that rapid actions of stress mediators might also facilitate, within a relatively short time window, memory retrieval processes. In particular, noradrenergic arousal has been associated with enhanced memory retrieval (Sara, 2009). For instance, stimulation of the locus coeruleus, the origin of noradrenergic forebrain projections, enhances retrieval in rats (Devauges and Sara, 1991). Similarly, the locus coeruleus is active during successful memory retrieval in humans (Sterpenich et al., 2006). Moreover, noradrenergic blockade impairs memory retrieval, both in humans and rats (Devauges and Sara, 1991; Kroes et al., 2010; Murchison et al., 2004). Based on these data, it can be hypothesized that, whereas stress-induced cortisol impairs retrieval, noradrenergic arousal may facilitate memory retrieval, particularly for information related to the stressful situation.

In the present experiment, we tested the hypothesis that stress may not necessarily impair memory retrieval and that stress-induced elevations in autonomic arousal and cortisol may have opposite effects on remembering. To this end, participants first learned neutral and emotional material. Twenty-four hours later, memory was tested either in a common free recall test (control condition) or in a stressful retrieval situation that resembled the well-known Trier Social Stress Test (TSST; Kirschbaum et al., 1993). Thus, in the 'retrieval-stress' condition, participants retrieved the learned material under stress, when autonomic arousal was high but cortisol concentrations not yet increased. Moreover, retrieval was a pivotal part of this stress situation and hence stressor-related. We predicted that autonomic arousal would enhance retrieval performance under stress. In order to contrast the hypothesized effects of autonomic arousal on retrieval with those of stress-induced cortisol, participants recalled part of the learned material after the stressor (or control condition), when cortisol concentrations were elevated. We expected that cortisol would impair memory retrieval, based on previous evidence (Buchanan et al., 2006; de Quervain et al., 1998, 2000). Moreover, because it has been shown that stress and glucocorticoid effects on memory are more pronounced for emotional than for neutral material (Buchanan et al., 2006; Cahill et al., 2003), we included both neutral and emotionally arousing stimuli and predicted that the effects of autonomic arousal and, in particular, those of cortisol would be stronger for emotional than for neutral stimuli.

2. Methods

2.1. Participants

Seventy-two non-smoking university students (36 men, 36 women; age: $M = 23.2$ years, SEM = 0.4 years) participated in this experiment. Exclusion criteria were checked in a standardized interview and comprised current illness or medication intake, current or life-time history of any psychiatric or neurological disorder, drug abuse, smoking, and in women the use of hormonal contraceptives. In addition, women were not tested during their menses. All participants provided written informed consent before participating in this study, which was approved by the local ethics committee.

2.2. Stimulus material

Stimulus materials consisted of 50 German nouns (25 neutral, 25 negative) and 50 pictures (25 neutral, 25 negative). Neutral and negative nouns were taken from a German database (Hager and Hasselhorn, 1994), based on their valence (neutral: $M = 4.17$, SEM = 0.03; negative: $M = 2.59$, SEM = 0.04, $p < 0.0001$) and arousal scores (neutral: $M = 3.78$, SEM = 0.07; negative: $M = 4.65$, SEM = 0.12, $p < 0.0001$), and matched with respect to word length ($p = 0.72$). Neutral and negative pictures were chosen from the International Affective Picture System (IAPS; Lang et al., 1997), according to their normative scores for valence (neutral: $M = 5.18$, SEM = 0.44; negative: $M = 2.45$, SEM = 0.66, $p < 0.0001$) and arousal (neutral: $M = 3.43$, SEM = 0.72; negative: $M = 5.88$, SEM = 0.73, $p < 0.0001$), and matched for their semantic categories (e.g. animals, humans). The pictures and words were not conceptually related.