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Research report



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HIGHLIGHTS

- The study investigated the effects of stress exposure on memory and startle.
- After the TSST participants remembered more central objects from the stressor.
- Startle responsivity was overall only descriptively enhanced.
- Startle responsivity to an odour ambient during the stressor tended to be enhanced.
- Commonalities and differences between immediate and delayed stress effects are discussed.

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ABSTRACT

Previously, we observed enhanced long-term memory for objects used (central objects) by committee members in the Trier Social Stress Test (TSST) on the next day. In addition, startle responsivity was increased. However, response specificity to an odour involved in the stressful episode was lacking and recognition memory for the odour was poor. In the current experiments, immediate effects of the stressor on memory and startle responsivity were investigated. We hypothesised memory for central objects of the stressful episode and startle response specificity to an odour ambient during the TSST to be enhanced shortly after it, in contrast to the control condition (friendly TSST). Further, memory for this odour was also assumed to be increased in the stress group. We tested 70 male (35) and female participants using the TSST involving objects and an ambient odour. After stress induction, a startle paradigm including olfactory and visual stimuli was conducted. Indeed, memory for central objects was significantly enhanced in immediate aftermath of the stressor. Startle responsivity increased at a trend level, particularly with regard to the odour involved in the stressful episode. Moreover, the stress group descriptively tended towards a better recognition of the odour involved. The study shows that stress enhances memory for central aspects of a stressful situation before consolidation processes come into play. In addition, results preliminarily suggest that the impact of stress on startle responsivity increases in strength but decreases in specificity during the first 24 h after stress exposure.

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1. Introduction

Stressful events can lead to long-lasting memories due to adaptive response mechanisms activated in a stressful situation. Stress induces rapid activation of the sympathetic nervous system (SNS)

http://dx.doi.org/10.1016/j.bbr.2017.03.002 0166-4328/© 2017 Elsevier B.V. All rights reserved. associated with increased vigilance and reduced executive control [1]. With a slight delay, the stress hormone cortisol is released through activation of the hypothalamus-pituitary-adrenal (HPA) axis. Cortisol initially potentiates the arousal-induced enhancement of basolateral amygdala activation via rapid non-genomic mechanisms, thereby enhancing memory consolidation [2]. Subsequently, cortisol reduces neuronal excitability via genomic mechanisms, causing a return to homeostasis [3]. This latter process reduces interference and further promotes long-term memory consolidation [4,5]. Particularly stress occurring within the learning context boosts memory for this event [5] and for potentially relevant items involved in the stressful situation [6].

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In humans, few studies have tested memory for experimentally induced stressful events [6,7]. While some studies resulted in impaired memory for stimuli experienced during stress [8] or reported general stress related memory impairments [9], others observed enhanced memories, especially for stressor-related stimuli [6,10,11] or pictures encoded during the stressful experience [12]. All of these studies tested delayed memory in a longer temporal distance to the acute stressor, when consolidation processes come into play and HPA activity restored to baseline. Memory for items related to the stressful situation has not yet been tested in the direct aftermath of the acute stress phase.

We recently compared memory performance of participants exposed to a psychosocial stressor (Trier Social Stress Test) [13] to that of participants exposed to a similar but non-stressful control condition (friendly TSST) [14]. In two independent studies, we could demonstrate that participants exposed to the stressful TSST, holding a free speech in front of a committee in a simulated job interview, performed better recognising central items (e.g. a rubber or a pen) which had been used by the members of the committee in a standardised fashion [6,14], on the next day. In contrast, there were no differences in recognition memory between the groups for peripheral objects (e.g. a mug or a ruler) which were also present on the table the committee was sitting at, but had not been used. As in the other studies mentioned before [6,10-12], memory was tested on the next day. It thus remained open whether this effect developed over time or might have been already detectable immediately after stress exposure.

In the acute stress phase, vigilance is increased to enhance attention for potentially relevant stimuli and to promote fast responses to the situation at hand [3]. This state leads to stronger responses particularly to negative stimuli in any sensory modality, e.g. a loud noise or a flash. Besides the immediate effects of stress on increased vigilance, long-term effects of stress on vigilance in terms of startle responsivity could be observed in the past. In a previous study, participants stressed with the TSST in a room with a previously neutral and unknown odour showed an enhanced startle response even 24 h after the stressful experience [15]. By applying a white noise burst via headphones, a startle eye blink reflex can be provoked whose amplitude or magnitude can be measured via electrodes attached to the eye muscle [16,17]. Being a well-established method for assessing implicit affective states, the fear-potentiated startle is often used to study the effects of valent stimuli or emotional conditions. Since negative stimuli presented during the startle procedure enhance the startle response [18–20], initially neutral stimuli associated with a stressful situation and the correspondent aversive state should have the potency to enhance the startle response like stimuli innately negative would do. The increased startle responsivity found in our previous study, however, was not specific to stimuli presented during the TSST (e.g. the ambient odour or the faces from the committee members), but was rather general and unspecific, indicative of increased anxiety [15]. This stronger responsivity at the expense of specificity was hypothesised to represent a functional shift in amygdaloidal activity [21]. Thus, a one-time laboratory stress experience apparently had the potency to activate an amygdaloidal pathway which was consolidated during a 24h time course and could pre-attentively be re-accessed by the startle procedure on the following day.

In contrast to this, in a previous study inducing stress with the Cold Pressor Test (CPT), diminished startle responsivity in the immediate aftermath of the stress induction was found [22]. The application of different stressors (CPT vs. TSST) might be responsible for the different results. Alternatively, acute stress might initially cause diminished startle responsivity, which, over a time course of 24 h, increases and eventually results in significantly enhanced startle responsivity. Moreover, it is unclear whether the response specificity towards stimuli experienced in the stressful context is increased in the immediate aftermath of the stressor.

Taken together, the described previous experiment from our laboratory is in line with the notion of enhanced memory consolidation and increased fearfulness after a single stress exposure, manifesting 24 h after the stressful event [15]. It is yet unclear whether this effect is indeed owed to a consolidation period or might also be observed in a startle paradigm administered directly subsequent to stress exposure. Causing a vigilant processing mode, stress should lead to an instant improvement of memory through its enhancing effects on memory encoding [1,23]. In contrast, the impact of stress on memory consolidation [24–27] suggests an enhancing long-term effect on the next day. Similarly, for effects of vigilance on the startle response, it is unclear whether startle specificity in response to stress-associated stimuli is increased in the immediate aftermath of the stressor, in contrast to 24 h later.

Given the rapid effects of stress on vigilance and attention, as well as previous findings of these effects and cortisol on startle responsivity [22,28], we intended to investigate short-term effects on the startle response during cortisol peak and on memory for stimuli experienced during the stressor in terms of visual object memory as well as olfactory memory immediately after the acute stress phase. Similar to our previous work [6,15], memory for the stressful episode and startle responsivity were assessed, this time focussed on effects after stress exposure at times of elevated cortisol concentrations. Memory retrieval took place approximately 40 min after termination of the stressor when stress impairs retrieval of stressor-unrelated material, such as peripheral objects in the TSST, whereas stressor-related memory contents are often unaffected [5,23,29]. Stress-induced physiological and psychological alternations (e.g. increased cortisol and increased negative affect) however still persist at that time after the stressor. We hypothesised that stressed participants would show an enhanced startle response specifically to the target odour and thus exhibit more specificity than 24 h later. Additionally, we presumed a better memory for the target odour in stressed participants. Moreover, stress is beneficial for memory when experienced during the learning episode (within the learning context [5,30,31]), which is the case in our study. Hence, for object memory it was hypothesised that enhanced vigilance caused by acute stress would be beneficial for free recall and recognition memory in the aftermath of the stressor, in particular for central objects.

2. Methods

2.1. Participants

We tested 70 non-smoking male (n=35) and female students from the Ruhr-University Bochum without any mental and physiological diseases and regular medication use. Females were only tested when having a regular menstrual cycle. Pregnant women, women during their menses, and those taking hormonal contraceptives were excluded [32,33].

The participants' age ranged from 18 to 33 years (M=23.59, SD=3.62) and their Body Mass Index from 18.07 to 28.99 (M=22.69, SD=2.63). For their participation, psychology students received course credits, and all others were paid an expense allowance of 20 \in . The study was approved by the local ethic committee of the Faculty of Psychology at the Ruhr-University Bochum, and the Declaration of Helsinki was followed.

2.2. Experimental session

Randomly assigned to either a stress or a control condition, participants underwent the Trier Social Stress Test (TSST) [13] or

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