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Research report

Enhanced memory for central visual and auditory elements experienced during a stressful episode

Tobias Rüttgens, Oliver T. Wolf *

Department of Cognitive Psychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr University Bochum, Germany

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ABSTRACT

Acute psychosocial stress has been shown to benefit memory for central visual elements of a stressful episode. Here, we aimed at investigating whether this effect is accompanied by improved visual memory for the committee members in a modified version of the Trier Social Stress Test (TSST). Specifically, we tested participants' recognition memory for accessories located on the bodies of the committee members, as well as their faces. Moreover, we investigated how stress influences memories for the content of the verbal interactions. That is, we studied how well participants remembered factual information associated with the main stress source, like name, age, and position of the committee members, as well as how accurately they could recite the exact wording of phrases used by them. In a counterbalanced 2 × 2 design, 77 men and women took part either in a stressful or non-stressful version of the TSST. While stressed participants better remembered personal information about the committee members than non-stressed participants, no differences in memory for the correct wording of phrases could be observed. Furthermore, in line with our hypothesis, stressed participants better remembered central, but not peripheral visual stimuli, compared to non-stressed participants, while, contrary to our expectations, stress did neither affect memory for objects located on the bodies of the committee members nor their faces. Our results are in line with the theory of enhanced memory binding under stress and extend previous results regarding improved memory for central visual elements encoded under stress to auditory learning material associated with the stressor.

1. Introduction

After being confronted with a stressor the autonomic nervous system (ANS) is activated. The ANS provokes a release of dopamine and noradrenaline in the prefrontal cortex which leads to increased vigilance and narrowed attention [1]. Next, the sympathetic-adrenal-medullary (SAM) axis is activated leading to a surge of peripheral adrenalin and noradrenaline [2] that affects, via the vagus nerve, hippocampus, amygdala, and prefrontal cortex [3]. Thereafter, the hypothalamic-pituitary-adrenal- (HPA) axis is activated. About 15–30 min after confrontation with a stressor, cortisol, the primary human glucocorticoid, is released into the bloodstream [2]. After crossing the blood-brain barrier, cortisol binds to receptors located in neurons in hippocampus, amygdala, and prefrontal cortex, thereby modulating neural activity in those brain regions [4,5]. By evoking an interaction of cortisol and noradrenaline, stress can alter neural activity in the basolateral nucleus of the amygdala [6,7]. The amygdala is the brain region that is responsible for giving memories their emotional quality [8]. These changes in neural activity initiate hippocampal plasticity and directly impact memory formation [9]. Thus, via the interaction of cortisol and noradrenaline in the basolateral amygdala, stress has the potential to influence memories.

Whether stress enhances or impairs memory formation seems to be dependent on the memory phase in which the organism is confronted with the stressor [10–12]. Stress that is experienced 20–30 min prior to encoding is suspected to undermine the process of long-term potentiation in the hippocampus, a mechanism essential for memorizing encoded learning material [13,14]. In contrast, stress experienced in the moment of exposure to the learning material, that is during encoding, benefits long-term potentiation processes and thereby improves memorization [15,16]. In the past, memory research has focused either on inducing stress before or after learning stress-related material, or on presenting unrelated verbal and visual learning material during a stressor [10,17]. More recently, however, it has been investigated how stress influences memories of the stressful event itself [18,19]. Increased levels of the stress hormone cortisol were associated with improved

* Correspondence to: Department of Cognitive Psychology, Ruhr University Bochum, Universitätsstraße 150, 44780 Bochum, Germany.
E-mail address: oliver.t.wolf@rub.de (O.T. Wolf).

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recognition memory for objects central to the stressful episode [18]. These findings are in line with the idea of enhanced memory binding under stress [20]. The more a certain detail is associated with the stress inducing event, the more likely it is to be remembered later. It has been suggested that relevance of the learning material to the stressor moderates the effect of stress on memory and that it might be more important than the delay between stress onset and encoding [21]. By influencing early attentional processes, stress enhances our memory for central items [22]. When salient elements of a situation elicit arousal, our attention narrows and shifts from the periphery, strengthening memories of these central aspects [23].

While there is ample evidence for a facilitative effect of acute stress on encoding of visual memories, little is known about how stress and thereof resulting hormonal changes affect auditory memories. In one study a film containing verbal information in the form of conversations between actors demonstrated that stress induction via a psychosocial stressor shortly after being exposed to the stimuli improved memory accuracy for the verbal information in question [24]. In a systematic review, Shields et al. [10] investigated how different sensory modalities (visual versus auditory) of learning material presented during a stressful episode influence the effects of acute stress on memory. They found no significant difference between visually and auditorily presented stimuli. Thus, it seems that acute stress facilitates auditory memories in the same way it improves memory for visual stimuli. While other studies utilized paradigms in which stress and encoding took place in spatial and temporal proximity as well [25], research investigating the accuracy of auditory memories of the stressful event itself is still lacking.

In the present study, we aimed at investigating whether the beneficial effect of acute stress on memory for central objects is accompanied by improved visual memory for the committee members in a modified version of the Trier Social Stress Test (TSST). Objects were divided into central and peripheral and placed on the table in front of the committee members. Additionally, we tested participants´ recognition memory for objects located on the committee members´ bodies (body objects) and their faces. Moreover, we investigated how stress influences memories of the content of verbal interactions. That is, we studied how well participants remember information like name, age, and position of the committee members, as well as how accurately they can recite the exact wording of phrases. Participants took part either in a stressful version of the Object-TSST [18] or a non-stressful control version [26]. We hypothesized participants taking part in the stressful version to have a higher increase of the stress hormone cortisol than participants taking part in the non-stressful version [26]. Regarding alpha-amylase levels, we predicted an increase in stressed as well as non-stressed participants [18,26]. Additionally, we expected an increase in negative affect in stressed, but not in non-stressed participants [18,26]. We hypothesized stressed participants to form more accurate memories of central objects, body objects, the committee members´ faces as well as of personal information mentioned by the members, but not of peripheral objects, than non-stressed participants [18,20].

This study has been preregistered at the Open Science Framework (https://osf.io/ek98g?view_only=61a6f027b0e94bf4b09e6b82f6fb1662).

2. Materials and methods

2.1. Participants

The target sample size was based on past relevant work [18,27] by averaging the effect sizes of the effect that corresponds to the interaction between item type and stress. By conducting an a priori power analysis using G*Power [28] for an ANOVA for fixed effects, special effects, main effects, and interactions (2 groups; 1 degree of freedom) with 80% power, an alpha of.05, and a medium effect size (f = 0.33), a target sample size of N = 75 was determined. We recruited 77 healthy men and women (39 men, 38 women) from Ruhr University Bochum through posters, handouts, social media, and online advertisement. Five participants had to be excluded because their baseline cortisol levels were more than three standard deviations higher than the mean. Our final sample thus consisted of 72 participants (37 men, 35 women).

Participants were between 18 and 33 years old ($M = 23.87$, $SD = 3.67$). Their Body-Mass-Index (BMI) ranged between 18.69 kg/m^2 and 30,03 kg/m^2 ($M = 23.13$, $SD = 2.8$). Before being invited to the laboratory, they underwent a standardized screening procedure via email or telephone. Participants with a BMI below 18 or above 30 kg/m^2 were excluded from the study. They had to be between 18 and 35 years old and were not allowed to be on medication, to suffer from a chronic disease, to use drugs or to smoke. Exceptional familiar or occupational stress, shift work four weeks leading up to the testing session, recent blood donation, and consumption of more than 15 alcoholic drinks per week were further exclusion criteria. Also, participants that had participated in the TSST before were not eligible for the study. Sex hormones can influence stress reactivity [29,30] and its effect on memory [31,32]. We therefore included exclusively women not using hormonal contraceptives and tested them preferably in the luteal phase. During the screening procedure women reported the date of their last and next expected menstruation, which allowed us to determine their respective cycle phase and schedule the testing session accordingly. Three of the 35 women (8,57%) were in the follicular phase when being tested, the remaining 32 (91,43%) in the luteal phase. We statistically checked whether the distribution of cycle phase between the groups was similar Results are reported in the results section under subheading 3.1.

Participants could choose between 30€ or 3 study credits for compensation. The study had been approved by the local ethics committee of the Faculty of Psychology and conducted in accordance with the Declaration of Helsinki.

2.2. Design and procedure

Participants were randomly assigned to two groups (stress vs. no stress). An equal number of men and women was exposed to each of the two conditions.

At the time of their arrival at the lab, participants did not know whether they had been assigned to the stressful or non-stressful control condition. Because cortisol naturally fluctuates over the course of a day, participants were tested between 12:30 pm and 17:15 pm [33]. On the first day, participants first signed the informed consent after being informed about their rights as participants, as well as the possibility that they might be asked to hold a free speech in front of a committee while being videotaped. Afterwards, they filled in a demographic questionnaire as well as the State-Trait Anxiety Inventory (STAI) [34] to control for symptoms of anxiety, before rating their current affect for the first time via the Positive and Negative Affect Scale (PANAS) [35]. Then, the first saliva sample was taken (baseline). Shortly before the start of either the TSST or the f-TSST, participants were informed about the condition they had been assigned to. This was meant to induce anticipatory stress in participants assigned to the stressful condition, while calming down participants assigned to the non-stressful control condition. After entering the room, participants had five minutes to prepare themselves, during which participants in the stress condition filled out the Primary Appraisal Secondary Appraisal questionnaire (PASA) [36] to induce further anticipatory stress. Afterwards participants were exposed to either the stressful or the non-stressful interview situation, during which they encountered the memory items. Once the interview was over, participants were brought back to the experiment room where they immediately delivered the second saliva sample (+1), after which they filled in a second PANAS questionnaire. Ten minutes later, participants delivered a third saliva sample (+10). They then engaged in a filler task not relevant for the present study. Thereafter, participants delivered the fourth and final saliva sample for the day (+25).

On the second day, participants first filled in another PANAS before delivering a fifth saliva sample. Afterwards, they engaged in the

recognition memory task. Finally, they were thanked, debriefed, and paid (Fig. 1).

2.3. Materials

2.3.1. Stress induction

In the regular version of the TSST [37] participants are supposed to hold a free speech talking about their personal strengths and engage in a mental arithmetic task in front of a reserved committee consisting of three people, all while being videotaped. This regular version has been modified in our lab previously [18]. This modified version introduced three main changes. First, our committee consisted of only two people (one male, one female). Second, the mental arithmetic part had been replaced by an additional three minutes of free speech. Third, the room in which the TSST took place was equipped with several objects, most of which were characteristic of an office and some of which were utilized by the committee members during the interview [18]. For the purpose of the current study, we modified this version of the TSST further. First, at the beginning of the interview the committee members shortly introduced themselves, mentioning their name, position, the institute they are employed at, and the research area they work in. Second, certain standardized phrases were articulated by the members over the course of the interview situation. The verbal information and objects served as recognition items. Details regarding memory assessment are provided in part 2.3.3 ("Memory").

The friendly-Trier Social Stress Test (f-TSST) served as a non-stressful control version of our modified version of the regular TSST and has been developed and utilized in our lab previously [26]. It applied the same basic interview situation with slight changes to the nature of the interview. Instead of applying for a job and talking about personal strengths, in the friendly version of the TSST participants were asked to talk about their hobbies and interests. The committee members were open, positive, and supportive. There was no videotaping [26]. These changes reduced the amount of uncontrollability and social evaluative threat, two factors that influence HPA-axis activity and result in higher cortisol levels [38]. For the purpose of the current project the friendly version of the TSST was modified in the same way as the stress-inducing version, the basic procedure and stimuli were the same.

2.3.2. Stress assessment

As a marker of HPA-axis activity, saliva samples were collected at five timepoints over the course of the testing sessions. Salivettes® (Sarstedt, Nümbrecht, Germany). Salivettes® were stored at −20 °C until assayed. Samples were analyzed with a time-resolved fluorescence immunoassay (IBL; Hamburg, Germany). All intra- and inter-assay coefficients of variations were below 10.16%.

Next to cortisol, salivary alpha-amylase was determined from the saliva as a biomarker of sympathetic response [39]. We applied a colorimetric test using the substrate reagent 2-chloro4-nitrophenyl-α-maltrotriosoide (CNP-G3). Intra- and inter-assay coefficients of variations were below 8%.

Affect was assessed via the German version of the PANAS [35]. Participants rated their current affect on a five-point scale consisting of a total of 20 items. These can be subdivided resulting in a positive affect (PA) value and a negative affect (NA) value.

2.3.3. Memory

In total, there were eight central objects, eight peripheral objects, eight body objects (four per committee member), eight personal information (four mentioned per member), and four standardized phrases. Objects were defined as central if they were interacted with by the committee members over the course of the interview situation [18,20,27]. Objects consisted of a stapler, a pencil, a pencil sharpener, a coffee mug, a beverage can, a stopwatch, a book, a garbage can, scissors, a hole puncher, a cup, a file folder, hand cream, a candy tin, a paper tray, and a handkerchief box. Body objects included a watch, a bracelet, a pen, and a lanyard. Additionally, the faces of the two committee members served as memory items. On the photos shown to the participants during the memory test, the members had a neutral facial expression. Moreover, the pictures were edited to ensure that only the faces, but not the hair or parts of the neck were visible [18,20,27].

Twenty-four hours after the first session, participants' memory performance was tested via a computerized recognition task. Photographs of the visual stimuli were presented next to the respective distractor items on a computer screen in front of a black background, without any additional contextual information. Auditory stimuli were presented in written form, with the personal information or phrase articulated by the committee members on the first day being presented next to the respective distractor information or phrase. We made use of a two-alternative forced choice (2AFC) recognition test in which participants had to decide for each stimuli pair which of the two memory items they had seen or heard 24 h before [40]. Instead of presenting the target item (object, personal information, etc.) next to a bogus item, we decided to create two versions of the TSST and f-TSST, each containing a different set of objects, body objects of the committee members, and semantic information. This way, we wanted to make sure that none of the memory items stood out in any meaningful way. The two versions were counterbalanced, in that half of the participants in each of the two conditions (stress vs. control) were exposed to either version. Our rationale behind this was to have a "truly" randomized paradigm. Which of the two

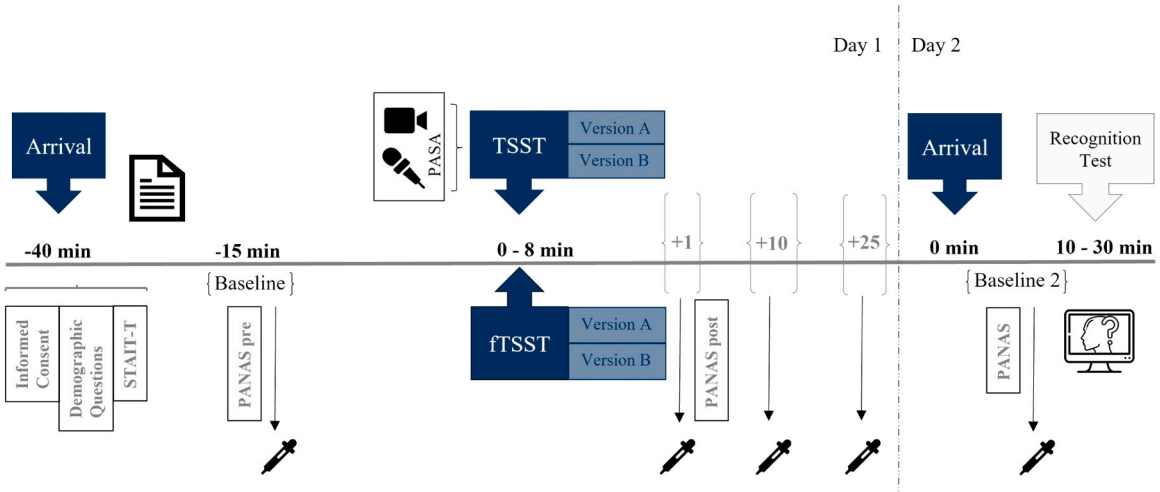

Fig. 1. Experimental procedure.

stimuli were presented on the left side and which on the right side was randomized as well, as was the order of the in total 36 questions.

2.4. Statistical analysis

All analyses were performed in IBM SPSS Statistics for Windows 21.0. The significance level was set to $\alpha = 0.05$; all post hoc tests were Bonferroni-corrected. In case the sphericity assumption was not met, Greenhouse-Geisser corrected values were reported. Analyses of variance (ANOVA) always included the between-subject factors stress (stress vs. control) and sex (male vs. female). Our hypothesis regarding the endocrine stress manipulation was tested with a repeated measures ANOVA which additionally included the within-subject factor time (baseline, −1, +1, +10, +25). For analysis of affect the factor time had two (before vs. after) levels. Our analyses regarding the effect of stress on memory for verbal information was tested with a two-way ANOVA. Lastly, our hypotheses regarding the effects of stress on memory for objects was tested with a three-way mixed ANOVA that included the additional within-subject factor item type (central- vs. peripheral- vs. body objects vs. faces). By means of an explorative analysis, we calculated correlation coefficients between participants' visual and auditory memory performance and the endocrine markers. For this, parameters for total salivary cortisol and alpha amylase output (area under the curve with respect to ground; AUCg) as well as increase (area under the curve with respect to increase; AUCi) were calculated [41].

To be able to compare the memory performance of stressed and non-stressed participants, we calculated $p(c)_{2AFC}$, a performance parameter of recognition. This parameter is formally equivalent to the sensitivity measurement Pr of the Two-High Threshold Model [42]. It assumes that response bias is negligible and was calculated as follows: p(c)2AFC = (HR + [1 − FA])/2. The hit rate was defined as the probability of correctly selecting the left stimulus on ⟨old, new⟩ trials (HR = p["left" | ⟨old, new⟩]), and the false alarm rate was defined as the probability of incorrectly selecting the left stimulus on ⟨new, old⟩ trials (FA = p["left" | ⟨new, old⟩]) [40].

3. Results

3.1. Sample characteristics

There were no significant differences regarding age, BMI, or symptoms of anxiety (all $F < 2.23$, all $p > .14$) between the two groups. A chi-square test demonstrated that there was no significant difference in distribution of cycle phase between the groups as well ($\chi 2[df = 1] = 0.37$, $p = .543$).

3.2. Stress manipulation

3.2.1. Salivary cortisol

Due to violation of normality, data were log-transformed. A significant main effect of the variable stress suggested that stressed participants responded with significantly higher cortisol levels than non-stressed participants ($F[1.81, 122.72] = 19.15$, $p < .001$, $\eta_p^2 = .22$). Moreover, a significant interaction between stress and time demonstrated that over the course of the testing session cortisol levels increased significantly more in stressed compared to non-stressed participants ($F[1.81, 122.72] = 18.24$, $p < .001$, $\eta_p^2 = .21$). All other effects were not significant (all $F < 1.63$, all $p > .203$). Post hoc analyses revealed that stressed participants had significantly higher cortisol levels at + 1 ($p = .004$), + 10 ($p < .001$) and + 25 ($p < .001$) min than non-stressed participants (Fig. 2A). At the start of the second session cortisol levels did not significantly differ between groups ($F[1,68] = 0.2$, $p = .653$).

3.2.2. Salivary alpha-amylase

Because alpha-amylase data were not normally distributed, we conducted our analyses with log-transformed data. A significant main effect of the variable time demonstrated that alpha-amylase levels increased in both groups over time ($F[2.14, 145.58] = 50.13$, $p < .001$, $\eta_p^2 = .42$). All other effects were not significant (all $F < 2.05$, all $p > .108$). Post hoc analyses indicated that participants' alpha-amylase levels significantly increased from baseline to + 1 ($p < .001$), and significantly decreased from + 1 to + 10 ($p < .001$). There was no significant difference in alpha-amylase levels between stress and non-stressed participants (Fig. 2B). At the start of the second session alpha-amylase levels did not significantly differ between groups ($F[1,68] = 1.42$, $p = .238$).

3.2.3. Affective stress response

As indicated by a significant main effect of the variable time ($F[1,68] = 6.48$, $p < .001$, $\eta_p^2 = .19$), significant interactions between the variables time and stress ($F[1,68] = 4.25$, $p = .043$, $\eta_p^2 = .06$) and time, stress and sex ($F[1,68] = 4.03$, $p = .049$, $\eta_p^2 = .06$) as well as significant corresponding post hoc tests non-stressed female participants had significantly higher positive affect scores after the f-TSST (3.53) as compared to stressed female participants (3.02; $p = .04$). For male participants no significant difference emerged (all $p > .691$). All other effects were not significant (all $F < 0.03$, all $p > .863$).

Regarding negative affect scores, a significant main effect of the variable time ($F[1,68] = 5.48$, $p = .022$, $\eta_p^2 = .08$), a significant interaction between the variables time and stress as well as thereupon conducted post hoc tests indicated that stressed participants had

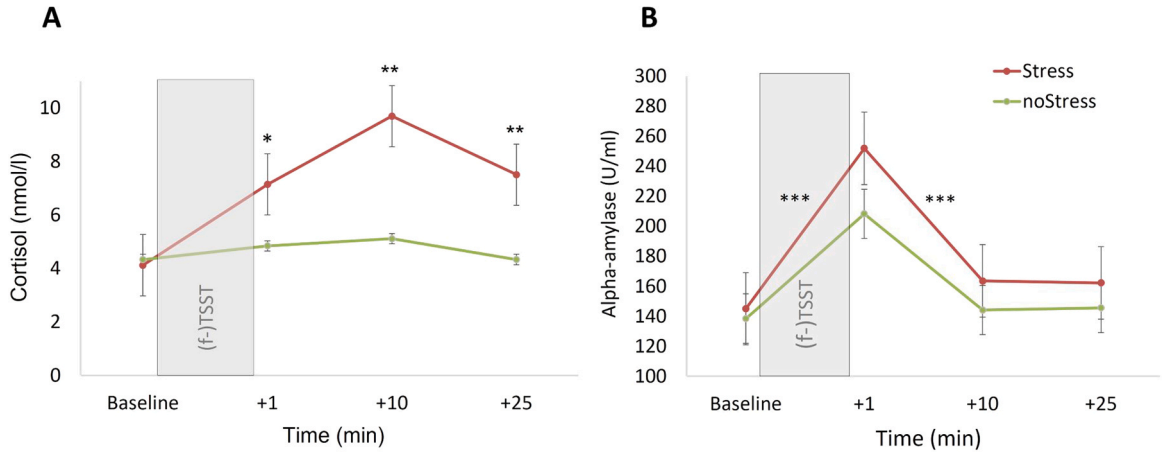

Fig. 2. Mean cortisol (A) and alpha-amylase (B) levels over the course of the testing session; (f-)TSST = (friendly-)Trier Social Stress Test; error bars represent standard errors of the mean; *** p < .001/** p < .01/* p < .05 compared to non-stressed participants.

significantly higher negative affect scores after the TSST (1.57) compared to non-stressed participants (1.19; $p = .001$). All other effects remained insignificant (all $F < 0.21$, all $p > .646$; Fig. 3).

3.3. Memory performance

3.3.1. Visual memory

Central objects were remembered better by participants, as indicated by a significant main effect of the variable item type ($F[1.81, 122.72] = 19.15$, $p < .001$, $\eta_p^2 = .22$). Furthermore, a significant interaction between the variables item type and stress ($F[1.81, 122.72] = 18.24$, $p < .001$, $\eta_p^2 = .21$) as well as subsequently conducted post hoc tests revealed that stressed participants better remembered central objects than non-stressed participants ($p = .004$). There were no significant differences regarding memory for peripheral objects, body objects or faces of the committee members (all $F < 1.73$, all $p > .194$; Fig. 4).

3.3.2. Auditory memory

Stressed participants remembered significantly more of the personal information mentioned by the committee members than non-stressed participants, as indicated by a significant main effect of stress ($F[1.81, 122.72] = 19.15$, $p < .001$, $\eta_p^2 = .22$). All other effects were not significant (all $F < 1.63$, all $p > .203$).

Exploratively, we had a look at our participants' memory for the four standardized phrases mentioned over the course of the interview. Due to late responses in the recognition task, 21 out of 288 answers (13,71%) could not be analyzed. No effect emerged as significant (all $F < 1.63$, all $p > .203$; Fig. 4).

3.3.3. Correlations

Exploratively, we calculated the correlation coefficients between the recognition memory marker $p(c)_{2AFC}$ for the different visual and auditory memory categories and total salivary cortisol and alpha amylase output (AUCg) as well as increase (AUCi). Neither individual salivary and alpha-amylase output nor increase predicted memory performance (all $F < 1.57$, all $p > .201$, all $R^2 < 0.12$).

4. Discussion

The goal of the study was twofold: first, we wanted to replicate the previously found effect that acute psychosocial stress improves memory for central visual elements of a stressful episode [18,20,27]. Second, we aimed at extending these results by investigating whether stress also benefits encoding of complex, auditory stimuli. We were able to replicate previous results by showing that stressed participants remembered more central visual elements compared to non-stressed participants.

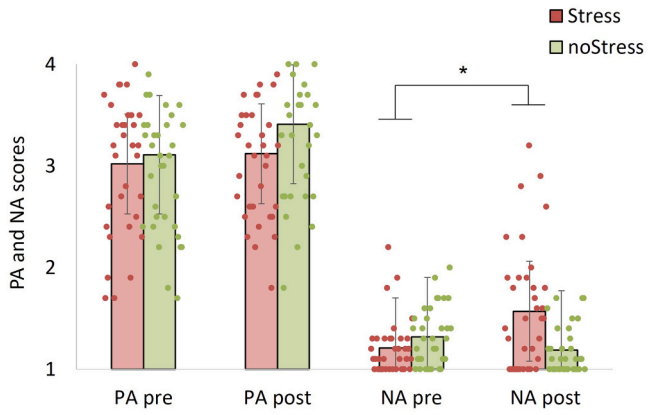

Fig. 3. Mean and individual positive (PA) and negative (NA) affect before (pre) and after (post) the (f-) TSST; * $p < .05$ compared to the pre-treatment measurement; see text for gender-specific results.

Furthermore, we were able to demonstrate that acute psychosocial stress at encoding improves memory for auditory elements of a stressful episode. Because these elements stood in direct relation to the main source of stress, namely the committee members, our results corroborate the theory of enhanced memory binding under stress.

Our stress manipulation was successful, both on the endocrine as well as on the affective level. As expected, participants taking part in the stressful version of the TSST had substantially higher cortisol levels after the procedure compared to participants taking part in the non-stressful control condition. In agreement with our hypothesis, salivary alpha-amylase levels increased comparably in stressed and non-stressed participants, indicating activation of the SNS. It has been shown that the SNS reacts in response to mild physical effort, like standing up and talking [39,43]. Still, it is noteworthy that participants taking part in the friendly version of the TSST reacted with a strong activation of the SNS, while their HPA-axis activity did not markedly change. Finally, stressed participants reported a profound increase in negative affect in response to the TSST, which points to a successful manipulation of our participants' affect.

In line with our hypothesis, stressed participants had better memory for central, but not peripheral objects, compared to non-stressed participants. This agrees with previous research on this topic [18,27] as well as the theory of enhanced memory binding under stress [21]. Long-term consolidation of emotionally arousing stimuli might be improved by amygdala activation, in that objects of central importance to a stressful situation may be encoded and consolidated preferentially. In contrast, connections between central elements of a stressful episode and other less important aspects or contextual details might not be consolidated to an equal degree [23]. This improvement of memory for central elements seems to be associated with altered neural representations in the amygdala. Bierbrauer et al. [20] were able to show that after encoding under stress central but not peripheral objects become more similar to one another as well as to the main stress source, the committee members' faces. While both the timing of the stressor as well as the relevance of the stimuli to the stressor play an important role in explaining the effect of memory binding under stress, it has been suggested that the latter might play a particularly prominent role [21,44].

Contrary to our expectations, acute stress did not significantly affect encoding of objects located on the bodies of the committee members and faces. Since these objects were part of the stress-inducing source, we hypothesized that they would be memorized better by stressed participants [12]. It is, however, possible that objects located on the bodies of the committee members are more comparable to peripheral rather than central objects, in that they are not interacted with and remain passive over the course of the interview. As described earlier, one prerequisite for emotional memory binding to take place is that stimuli are perceived to be of central importance for the stressful situation [21], a precondition which might not have been met in case of the body objects. Thus, centrality seems to refer primarily to the binding between stimuli and the stress source, instead of the two being in close spatial and temporal proximity. Alternatively, the absence of an effect of stress on memory for body objects could be explained via stressor-specific patterns of attentional avoidance. Next to its influence on memory formation, stress has the potential to alter fixation behavior. During times of stress, people tend to avoid gazing at socially threatening stimuli, for instance faces of people involved in the stress inducing situation [45]. In situations involving immediate social evaluative threats, for instance in an interview situation, gaze avoidance is more likely to occur [46]. In a study by Herten et al. [45] that investigated the effect of stress on fixation behavior, members of the stress group indeed fixated the faces of the committee members less often but spend more time fixating central objects. Importantly, however, fixation indices were not associated with any of the obtained memory measures.

To the best of our knowledge, our study was the first to demonstrate that acute psychosocial stress at encoding improves memory for auditory elements of a stressful episode. Because the auditory stimuli

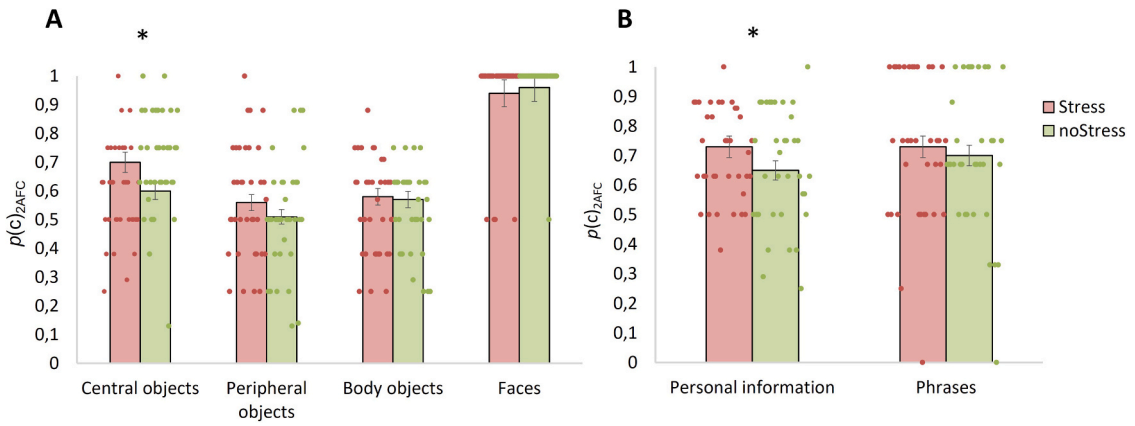

Fig. 4. Mean and individual recognition performance of visual (A) and auditory (B) stimuli; visual stimuli were divided into central and peripheral objects as well as of body objects and faces of the committee members; auditory stimuli consisted of personal information and standardized phrases; error bars represent standard errors of the mean; * $p < .05$ compared to non-stressed participants.

consisted of personal information mentioned by the committee members, they might have been perceived by the participants to be directly related to the main stress source. In that sense, encoding of the personal information was affected by stress the same way central visual objects were. While the effect of acute psychosocial stress at encoding on memory for complex auditory stimuli had not been investigated before, our results are in line with a meta-analysis by Shields et al. [10]. The authors investigated which factors affect the relationship between acute stress and memory formation. They found that the sensory modality of the stimulus presentation did not significantly moderate the effects of acute stress on memory formation. Encoding of learning material presented via the auditory modality is thus equally likely to be enhanced by acute stress than visually presented stimuli [10]. While personal information about the committee members were remembered better by stressed as compared to non-stressed participants, such a difference in memory performance was not observed for the standardized phrases. It is plausible that a differentiation between central and peripheral stimuli can be made for auditory stimuli as well. Because the phrases were not directly connected with the committee members, other than being articulated by them, it is possible that participants did not perceive them to be of central importance for the stressful situation, preventing processes of emotional binding necessary for enhanced memory formation to take place. Moreover, the personal information were articulated at the beginning of the stressor when ANS and SMA activity still dominates [47]. The standardized phrases, on the other hand, were mentioned at the start as well as towards the end of the TSST, half of them were thus encoded under increased cortisol levels. This is in line with the "temporal dynamic model of emotional memory processing" proposed by Diamond and colleagues [48]. After an initial phase of enhanced long-term potentiation (LTP), the hippocampus enters a state of reduced potential for LTP caused by a reduction in NMDA-receptor sensitivity. It is possible that the last two standardized phrases were encoded primarily during the second phase, which could explain why only memory for the personal information benefitted from the enhanced memory formation under stress. Furthermore, while glucocorticoids seem to contribute to memory generalization, norepinephrine, which is active primarily during the first phase of the TSST, is assumed to benefit memory accuracy, by increasing connectivity between the amygdala and hippocampal regions [49]. Despite significant group effects of stress on central memories, endocrine markers (cortisol and alpha-amylase) and memory measures were not significantly correlated. This might reflect the complexity of the observed processes as well as interindividual differences in stress responsivity and sensitivity [50]. Noteworthily, a previous study with a comparable design [18] as well as a large meta-analysis [10] were not able to show significant correlations between endocrine markers and memory, either.

While our study offers novel insides into the effects of stress at encoding on memory formation, our methodology is not without limitations. First, as participants encountered the personal information and phrases via the auditorily modality and were exposed to them in written format during the recognition paradigm, encoding and retrieval took place in a cross-modal fashion. While having our participants encode the learning material in one modality and retrieving in another might not have been optimal, as processing of auditorily and visually presented learning material differs [51], we nevertheless were able to find a significant effect of stress on memory for auditorily presented stimuli, which speaks for the robustness of the effect. Second, due to limitations of practical implementation, the number of memory items for each separate category was relatively low (ranging from 8 to 2). A low number of memory items might pose reliability issues, as it makes memory data noisier and requires larger sample sizes to reduce the risk of committing measurement errors [52]. This was specifically the case for face stimuli, as there where only two faces to remember and almost all participants were able to recognize them correctly. As participants in both groups were able to correctly recognize the committee members faces in well over 90% of cases, we suspect that memory data concerning face stimuli might additionally be affected by a presumed ceiling effect. Thus, with our study design it was not possible to detect a potential effect of acute stress on encoding of facial stimuli. In the study by Wiemers et al. [18] stressed participants better remembered the committee members' faces than non-stressed participants. While their design was similar to ours, they applied a yes-no-recognition paradigm, which is considered to be more difficult than the 2AFC paradigm we used. A yes-no paradigm might thus be more suitable to investigate the effect of stress on memory for faces. While there have been studies investigating how acute stress during encoding affects later face recognition [53], there is a need for study designs incorporating naturalistic facial stimuli as part of the stress inducing event. A modulated version of the TSST in which more people than just the committee members take part could be developed. Additionally, a larger number of distractor stimuli could further increase difficulty of the recognition task which might prevent a potential ceiling effect. Lastly, studies utilizing the TSST in its virtual reality (VR) version, namely the TSST-VR [54], might incorporate substantially larger numbers of committee members, thus increasing the number of potential face stimuli.

5. Conclusion

The current study investigated how an acute psychosocial stressor influences the encoding of central visual and auditory elements of the stressful episode. While replicating previously shown beneficial effects of stress on memory for visual stimuli, our study was the first to extend

these findings to auditory learning material. It seems that the effect is not specific to one sensory modality but rather governed by central physiological mechanisms affecting processes of memory formation regardless of the learning modality. While demonstrating this effect utilizing complex, realistic auditory stimuli, is a valuable first step, more research on this topic is needed. Future studies should aim to replicate our results by applying a comparable methodology while implementing auditory stimuli of different types, complexities and quantities into the stress inducing paradigm. Also, further learning modalities like kinesthetic and tactile learning could be investigated in the context of acute stress.

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CRediT authorship contribution statement

Tobias Rüttgens: Conceptualization, Formal analysis, Writing – original draft, Visualization. **Oliver T. Wolf:** Funding acquisition, Conceptualization, Supervision, Writing – review & editing.

Declaration of Competing Interest

All authors declare no conflict of interest.

Data availability

Data will be made available on request.

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