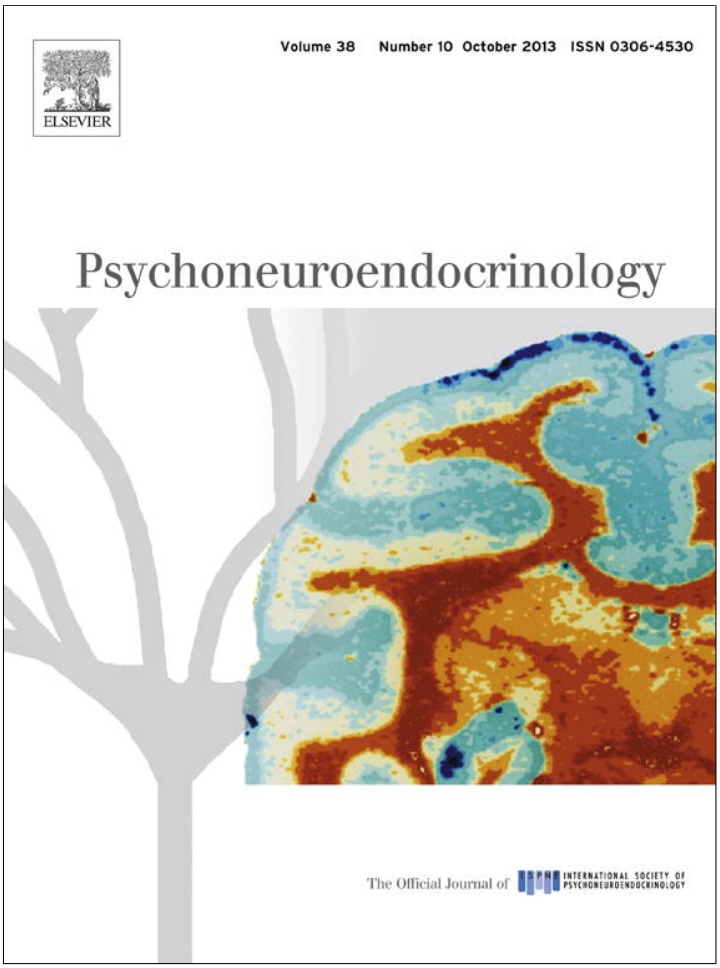

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What we remember from a stressful episode

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Summary A stressful episode is thought to be consolidated better because of a stress-induced activation of the hypothalamus—pituitary—adrenal (HPA) axis. However, human experimental studies addressing this hypothesis directly are lacking. Thus, we investigated memories of the stressful episode itself. Furthermore, we aimed to determine the influence of stress on recollection and familiarity processes. Participants ($n = 63$) were subjected to a psychosocial stressor (Trier Social Stress Test, TSST) or a newly developed non-stressful control condition (friendly-TSST). During both conditions, they were exposed to a committee and visual stimuli, either bound to the situation (central) or not (peripheral). The next day, participants engaged in unexpected recognition tasks.

Negative affect and salivary cortisol concentration increased in stressed but not in control participants. The following day, stressed participants recognized central objects and the committees' faces better than control participants. Furthermore, recollection contributed significantly more to memory performance in stressed than in control participants.

Our findings are congruent with the idea of enhanced memory binding under stress combined with enhanced memory consolidation of information acquired during stress. What we remember from a stressful episode appears to be determined by the strength of the association between the stressor and the material to be remembered.

1. Introduction

It is widely accepted that stress enhances memory consolidation by activation of the sympathetic nervous system (SNS) and the hypothalamus—pituitary—adrenal (HPA) axis (Diamond et al., 2005; Joels et al., 2011; Roozendaal and McGaugh, 2011). Main support for this hypothesis comes from rodent studies. Making a memory task more stressful enhances the memories of it, leading to enhanced performance 24 h later (Akirav et al., 2004). Based on findings like this, the notion has arisen that stress needs to occur within the learning context in order to lead to memory enhancement (Joels et al., 2006), or at least in close temporal proximity to the material which is supposed to

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be remembered (Diamond et al., 2005). Research by Roozendaal and McGaugh has helped to elucidate the underlying mechanisms (Roozendaal and McGaugh, 2011). Noradrenergic arousal followed by a glucocorticoid (GC) signal causes enhanced activity in the basolateral amygdala (BLA). This, in turn, enhances memory storage in the hippocampus. Somewhat surprisingly, this assumption has not yet been tested experimentally in humans. Most studies assessing memory performance under stress in humans have concentrated on inducing stress before or after learning of stress-related material (Schwabe et al., 2008; Smeets et al., 2009), or presented verbal or visual material during a stressor (Henckens et al., 2009; Schwabe and Wolf, 2010). However, so far, few experimental studies have assessed memory for the stressful event itself (Rimmele et al., 2009; Quas et al., 2010, 2012). Rimmele and colleagues assessed the effects of melatonin administration on memories of a stressful episode. However, in their study, a stress-free control condition was missing. The same holds true for the studies by Quas and colleagues. Using correlations, they found that an increase of cortisol concentration was associated with a better memory for the stressful episode (Quas et al., 2010, 2012) as assessed by open-ended questions. In one study this effect was only observed in children (Quas et al., 2010), in another study this held true especially if sympathetic arousal was also heightened (Quas et al., 2012). Both studies suggest that memories of a stressful episode are remembered especially well. However, since none of these studies included a control condition, causal conclusions were precluded.

Eyewitness and flashbulb memory studies show that arousing events are indeed remembered well (Christianson, 1992). They are, however, rather descriptive in nature. Moreover it is unclear exactly which aspects of a situation will be consolidated and remembered better under the influence of stress or arousal. Literature from research on emotional memories could provide some guidelines. Emotional stimuli are generally remembered better than neutral ones. This has been associated with an involvement of the amygdala and its interaction with the adjacent hippocampus (Cahill and McGaugh, 1998; LaBar and Cabeza, 2006). Different hypotheses propose exactly which aspects will be remembered from an arousing situation. Most postulate that the processing and remembering of central cues will be enhanced under emotional arousal (Easterbrook, 1959; Mather, 2007; Kensinger, 2009; Waring and Kensinger, 2011). According to some hypotheses, the processing of peripheral cues will be impaired (Easterbrook, 1959; Kensinger, 2009; Waring and Kensinger, 2011), while according to others, the processing of peripheral cues might not be influenced by emotional arousal at all (Mather, 2007; Steinmetz and Kensinger, 2013).

Typically, memory performance is assessed by free recall or by recognition tasks. While participants have to generate the memory independently in free recall tasks, they have to decide whether they have or have not encountered a given item in recognition tasks. Recognition memory can be divided into recollection and familiarity. Recollection is an active retrieval process wherein participants are able to access detailed information of when and where an item was encountered. Familiarity is a vague feeling of knowing an item without access to associated details (Yonelinas, 2002). According to some researchers, recollection and familiarity lie on a continuum and differing in the strength of the memories only (Wixted, 2007). In contrast, according to the dual-process model, both processes are functionally and structurally distinct. According to this view, recollection is thought to rely on the hippocampus and familiarity on parahippocampal regions (Eichenbaum et al., 2007; Sauvage et al., 2008). Evidence exists that stress has a differential effect on recollection and familiarity (Yonelinas et al., 2010), which would corroborate the view that recollection and familiarity are distinct processes. Since GCs are thought to exert their actions predominantly in the hippocampus (de Kloet et al., 1998), we expect stress to primarily influence recollection. Receiver operating characteristic (ROC) curves are a useful method to analyze the contribution of recollection and familiarity to recognition memory (Yonelinas and Parks, 2007).

In order to determine exactly what will be remembered from a stressful episode and how stress influences recognition memory for the stressful episode, the current study investigated memory performance for visual objects encountered during a stressor (Trier Social Stress Test; TSST; Kirschbaum et al., 1993) and compared that to memory performance for the same objects encountered during a non-stressful but matching control condition (friendly-TSST; Wiemers et al., 2013). Besides the usually found stress reactions, we hypothesize that stressed participants have a more accurate memory than non-stressed participants for central visual details. Furthermore, stress should specifically enhance recollection.

2. Methods

2.1. Participants

Participants included 63 healthy adults (32 males) between 19 and 30 years of age. The current sample is an expansion of that described in the method paper about the friendly-TSST (Wiemers et al., 2013). General exclusion criteria were former participation in the Trier Social Stress Test (TSST), a BMI under 18 or over 30, receiving medical treatment, taking medication influencing the HPA axis, and smoking. Pregnant women and women taking oral contraceptives were excluded from participation as well. Testing of women was scheduled outside of menses. Participants received a compensatory payment of 25€. The study was approved by the local ethical committee of the Faculty of Medicine of the Ruhr-University Bochum. The declaration of Helsinki was followed.

2.2. Material

2.2.1. Hormonal assessment

Participants were instructed to refrain from eating or drinking anything but water 1 h before testing and from doing excessive sports, drinking alcohol, or taking medication the day before testing. Saliva for hormonal assessment was sampled using Salivettes® (Sarstedt, Germany) four times on the first testing day and about 24 h later on day 2. Cortisol was analyzed by an immunoassay (IBL, Hamburg, Germany). Inter- and intra-assay variabilities were below 10%. Salivary alpha-amylase (sAA) was analyzed by a quantitative enzyme

kinetic method as described elsewhere (Rohleder and Nater, 2009).

2.2.2. Affect rating

By means of the self-rating scale "Positive and Negative Affect Scale" (PANAS; Watson et al., 1988) participants rated their current affect on a five-point scale for 20 items. These can be subdivided resulting in a positive affect (PA) value and a negative affect (NA) value. Participants completed the PANAS twice on day 1 and once on day 2.

2.2.3. Stress procedure

2.2.3.1. TSST. The Trier Social Stress Test (TSST) is a standardized psychosocial laboratory stressor that leads to a reliable stress response of the SNS and the HPA axis (Kirschbaum et al., 1993). In its original form, it consists of three parts: a preparation time of 5 min, a 5 min free speech about personal characteristics in front of a two-person committee wearing white lab coats and acting neutral and reserved, and a 5 min mental arithmetic task. During the latter two tasks participants are videotaped. For the purpose of assessing memory for the stressful situation in this study, the stressor's structure had been modified. During the first 5 min participants filled in a sham questionnaire to increase ego-threat, and were instructed to prepare their speech. Next, they were requested to hold a free speech about their personal characteristics in a sham job interview for 8 min in front of a committee acting neutral and reserved (one male and one female). During the latter task participants were videotaped.

Furthermore, the TSST room had been equipped with 16 office objects (e.g. a stapler, a book). Eight of these objects were used by the committee in a standardized sequence (afterwards referred to as central objects).

2.2.3.2. friendly-TSST. To create a well-matched, non-stressful control situation to the modified TSST, the friendly-TSST (f-TSST) was developed (for a detailed description see Wiemers et al., 2013). As opposed to other non-stressful control conditions (Het et al., 2009), we needed a committee which adhered to the same timing procedure as in the TSST, including the interaction with the objects. During a 5 min preparation time, participants made notes about their school years and university track, career aspirations, hobbies, and favorite book or movie. Afterwards, participants stood in front of the committee and talked freely about their life and career aspiration for 8 min. The committee reacted friendly by nodding and smiling to give participants a feeling of safety. There was no videotaping during the f-TSST.

2.2.4. Recognition objects

During the stress or control procedure, 16 objects were present in the room. Eight of these (pencil, pencil sharpener, stop watch, plastic cup, water bottle, candy tin, stapler, paper tray) were interacted with during the TSST/f-TSST by the committee in a standardized sequence, without notifying participants explicitly about this. For example, one committee member briefly sharpened a pencil. These manipulated objects were thus directly associated or bound to the main stressor of the paradigm. These objects were designated as central objects. Eight objects were not used by the committee and were thus designated as peripheral objects (hole puncher, book, file folder, scissors, handkerchiefs, coffee cup, dustbin, and highlighter). The terms central and peripheral as used here do not refer to spatial localization of the objects but rather to the role of the object during the situation.

Pictures of these objects served as target pictures in a recognition task. Pictures of 32 other objects served as distractor stimuli. The distractors consisted partly of the same objects as the target objects, but differing in color or shape, and partly of completely different objects. Pictures of the committee members' faces were included in the recognition task as well, while 3 additional pictures of faces served as distractors.

2.2.4.1. Object recognition task. On the second day, participants saw pictures of objects on a computer screen in a randomized order. Each picture was presented for 2 s and followed by a screen asking the participants to rate how sure they were of whether or not they had seen this exact object in the TSST/f-TSST room on a six point scale ranging from *very sure of having seen the object* to *very sure of not having seen the object*. This rating scale is essential for ROC analyses (Yonelinas and Parks, 2007). Participants had 5 s to rate each picture by pressing a button. If they did not answer during this period, no answer was recorded and the program proceeded. Preceded by a short blank screen and a fixation cross (1 s each), the next picture was presented.

2.2.4.2. ROC analyses. ROC curves are, on the one hand, defined by asymmetry, the height of the *y*-intercept which indicates a measure of recollection (the higher the *y*-intercept, the stronger recollection is present). On the other hand, the curves are defined by the curvilinearity, which is a measure of familiarity (the more curvilinear a ROC curve, the more familiarity is present). Typically, recognition memory for single items is comprised of both recollection, expressed by a ROC curve with a *y*-intercept significantly higher than 0, and familiarity processes, expressed by a curvilinearity higher than 0. If, however, the curve is asymmetric but linear, this indicates that the contribution of familiarity is negligible and points to associative memory processes (Yonelinas, 1997).

2.3. Procedure

On the first day, participants first signed informed consent and were hereby informed about the possibility of having to give a talk in front of a committee and a video camera, group affiliation was disclosed after the baseline saliva sample. Afterwards, participants engaged in a story writing exercise irrelevant for the current report. Forty minutes after arrival, participants rated their current affect by filling in the "Positive and Negative Affect Scale" (PANAS; Watson et al., 1988), and delivered the first saliva sample (baseline). Next, the experimenter brought the participant to the room in which the stress induction or control condition was conducted, thereby exposing participants to the recognition objects. Group assignment (stress or control condition) was random. After the procedure, participants were brought back to the experiment room. They immediately delivered the second saliva sample (+1), then filled in the PANAS and another

questionnaire about handedness irrelevant for current purposes for 10 min until the next saliva sample (+10). After this, participants completed a dichotic listening task irrelevant for current purposes for 15 min before delivering the last saliva sample (+25). At the end of testing on day 1, the standardized stressor was revealed to have been a standardized situation. Importantly, participants were never alerted that their memory for the stress or control condition would be assessed on the next day.

On day 2, approximately 24 h later, participants came back to the lab. They first filled in the PANAS and another questionnaire irrelevant for the current report (questionnaire assessing perfectionism). Next, the last saliva sample (T2) was delivered before performance of the recognition task. Finally, participants were thanked, debriefed, and paid.

Since cortisol follows a circadian rhythm, all testing was carried out in the afternoon starting between 1.45 p.m. and 3.30 p.m. on the first day and starting between 1 p.m. and 5 p.m. the second day.

2.4. Statistical analyses

We examined all dependent variables for normality and, if it was violated, log-transformed data. Cortisol and sAA were analyzed with a repeated measures analysis of variance (ANOVA) with TIME of measurement as within-subject factor (baseline, +1, +10, +25) and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors. If sphericity was violated, Greenhouse Geisser-corrected p-values are reported. To examine the specific hypotheses stated in the introduction, planned comparisons examined group differences in cortisol after the TSST or f-TSST.

Mean values for PA and NA were calculated (mPA, mNA) and analyzed with a repeated measure ANOVA with TIME (pre, post) and AFFECT TYPE (positive, negative) as within subject-factors and STRESS (stress vs. control) and SEX (male vs. female) as between subject factors. Planned comparisons examined group differences in negative affect after the TSST or f-TSST.

In order to reveal group differences in object recognition performance, answers in the object recognition task were dichotomized into ''seen the object during the procedure'' (''yes'') and ''not seen the object during the procedure'' (''no''). Hit rates (HR) and false alarm rates (FA) for central and peripheral objects were calculated. To obtain a memory performance measure of recognition (Pr), FA was subtracted from HR according to the Two-High Threshold Model (Snodgrass and Corwin, 1988; Corwin, 1994). Object recognition for Pr was analyzed with a mixed model ANOVA with OBJECT TYPE (central, peripheral) as within-subject factor and STRESS (stress vs. control) and SEX (male vs. female) as between subject factors. Planned comparisons examined whether the groups differ in recognizing central visual details. To further unravel the effect, the same ANOVAS were carried out for HR and FA separately. Since we did not have a priori hypotheses, post hoc t-tests were corrected for multiple comparisons with the Bonferroni–Holm method.

For the purpose of assessing whether recollection (R) and familiarity (d') were differentially influenced by stress, ROC analyses were performed on the object recognition task including the objects and faces (Yonelinas, 1994). In order to draw the curves, the probability of hits was plotted against the probability of false alarms across five cumulated bias levels (Yonelinas and Parks, 2007). A curve for each participant was generated by an excel solver using the method of least-squares (Yonelinas, 1997). Afterwards, individual curves were examined for a bad spread (meaning participants did not use the whole answer scale) and to check whether answer level was at chance level. A bad spread of answers and an answer level at chance level would both constitute a curve which does not allow for an analysis of recollection and familiarity. Thus, these curves were excluded. Data was z-transformed by taking the inverse of the standard cumulative normal distribution of each hit and false alarm rate in order to analyze data in a model independent way. Linear and polynomial regressions were fitted to each individual performance and R^2 were compared by dependent t-tests for polynomial and linear regressions for the stress and control groups separately. A better polynomial fit would suggest a linear curve in ROC space, i.e. associative memory model, while a better linear fit would suggest a curvilinear curve in ROC space, i.e. item memory model. According to these results, the appropriate model was chosen for analyses in ROC space. A measure for recollection (R) is reflected by the y-intercept of the ROC curves and a measure for familiarity (d') is derived from the distances between the means of the old and the new item distributions (Yonelinas, 1997). These measures were compared between stress and control groups by independent t-tests. In order to analyze directly whether stress had a differential effect on recollection and familiarity, d' was converted from the distance measure into a probability estimate of familiarity (F). A mixed model ANOVA with PARAMETER ESTIMATE (R, F) as within-subject factor and STRESS (TSST vs. f-TSST) as between-subject factor was followed by a planned comparison comparing R for the TSST and f-TSST groups.

An overall alpha level of $p < .05$ was applied.

3. Results

3.1. Participants

Datasets of three participants were excluded from all analyses, one dataset due to an illness on the second test day, one due to insufficient language proficiency, and another due to outlier values in salivary cortisol (more than 1.5 interquartile-ranges above the upper quartile). Sixty participants (30 males) were left in the analyses. Table 1 shows demographic characteristics of the sample.

3.2. Stress measures

3.2.1. Salivary cortisol

Analyses of cortisol responses to the stress or control procedure included 58 participants for day 1 and 54 for day two due to missing cortisol data (insufficient amount of saliva collected and/or sample contamination).

A repeated measures ANOVA with TIME of measurement as within-subject factor (baseline, +1, +10, +25) and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors was conducted. Since Mauchly's Test revealed a violation of sphericity ($\chi^2(5) = 81.56$, $p < .001$), Greenhouse

Table 1 Demographic characteristics and salivary alpha-amylase of the sample split for group assignment; numbers represent mean ± standard deviation; TSST = Trier Social Stress Test; BMI = Body Mass Index (weight in kg/(height in cm)^2); sAA = salivary Alpha Amylase (log transformed values in Units per liter).

	TSST	friendly-TSST	Total group
N	30	30	60
Males/females	15/15	15/15	30/30
Age in years	23.93 ± 2.59	23.8 ± 2.29	23.87 ± 2.43
BMI	22.23 ± 2.37	22.09 ± 3.00	22.16 ± 2.68
N	29	21	50
sAA baseline	1.36 ± 0.48	1.43 ± 0.36	1.39 ± 0.43
sAA + 1	1.80 ± 0.41	1.80 ± 0.59	1.80 ± 0.49
sAA + 10	1.39 ± 0.45	1.51 ± 0.38	1.44 ± 0.42
sAA + 25	1.46 ± 0.34	1.41 ± 0.64	1.44 ± 0.48

Geisser corrected *p*-values (ε = .51) are reported. Cortisol concentrations in stressed participants increased in response to the stressor, whereas cortisol concentrations in non-stressed participants slightly decreased in response to the control condition (see Fig. 1). This was reflected in a significant TIME × STRESS interaction effect ($F(3,162) = 30.85$, $p < .001$) and a significant main effect of TIME ($F(3,162) = 21.88$, $p < .001$) as well as in a significant main effect of STRESS ($F(1,54) = 11.20$, $p = .001$). Planned comparisons revealed no significant differences of salivary cortisol levels between groups at baseline ($t(56) = -.34$, $p = .73$), but significant differences at time +1 ($t(56) = 2.46$, $p = .017$), +10 ($t(56) = 5.07$, $p < .001$; corr.), and +25 ($t(56) = 4.61$, $p < .001$; corr.). There were no effects of SEX (all *p*'s > .20).

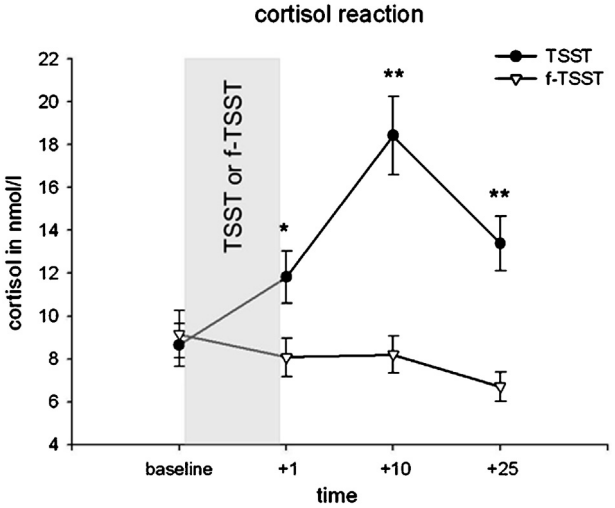

Fig. 1 Salivary cortisol. Mean values (±standard error of mean) of salivary cortisol in nmol/l of the stress (TSST) and control (f-TSST) groups directly before (baseline) and 1 (+1), 10 (+10) and 25 (+25) min after the cessation of the procedure; TSST = Trier Social Stress Test; f-TSST = friendly-Trier Social Stress Test; the procedure itself took approx. 15 min; stressed participants displayed increased cortisol concentrations, while no changes in cortisol concentrations were observed in the control group; significances refer to comparisons between TSST and f-TSST group: $^{**}p < .001$; $^{*}p < .05$.

Group comparisons for salivary cortisol at day 2 revealed no significant differences between groups (stress: MW = 7.38, SE = 0.56; control: MW = 8.07, SE = 0.82; $t(52) = -.704$, $p = .485$).

3.2.2. Salivary alpha-amylase

Analyses of sAA were conducted with 50 participants due to missing data and outlier values. Results are reported in Table 1. A repeated ANOVA with TIME of measurement as within-subject factor (baseline, +1, +10, +25) and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors was conducted with log-transformed data due to violation of normality. Salivary AA increased in response to both conditions (TSST and f-TSST), which did not differ from each other. This was reflected in a significant effect of TIME ($F(3,138) = 17.39$, $p < .001$). There were no further significant main or interaction effects (all $p > .05$). On day 2 there were no significant differences in sAA between groups ($t(52) = -.59$, $p = .58$).

3.2.3. Affect rating

Since mNA values were not normally distributed, data was log-transformed. A repeated measures ANOVA with TIME of measurement (before, after) and AFFECT TYPE (positive, negative) as within-subject factors and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors was conducted.

Results show a significant three-way interaction TIME × AFFECT TYPE × STRESS ($F(1,58) = 11.61$, $p = .001$), significant two-way interactions TIME × STRESS ($F(1,58) = 4.72$, $p = .034$), and AFFECT TYPE × STRESS ($F(1,58) = 13.56$, $p = .001$) as well as a significant main effect of AFFECT TYPE ($F(1,58) = 293.25$, $p < .001$). According to our hypothesis, we especially wanted to follow up effects of stress on negative affect, thus data was split for affect (positive and negative). A 2-way ANOVA was carried out for each affect type with TIME as within-subject factor and STRESS as between-subject factor. Results show that negative affect increased in the stress group but not in the control group in response to the respective procedure. This was reflected in a significant TIME × STRESS interaction effect ($F(1,58) = 13.45$, $p = .001$) and a significant main effect of STRESS ($F(1,58) = 12.99$, $p = .001$). There was no main effect of TIME ($p > .10$). Planned comparisons revealed higher negative affect in participants after stress (MW = 0.19, SE = 0.03) than in participants after the control condition (MW = 0.04, SE = 0.01; $t(58) = 4.41$, $p < .001$; corr.) but no group differences before the respective procedure (TSST: MW = 0.12, SE = 0.02; f-TSST: MW = 0.09, SE = 0.02; $p > .10$). On day 2 groups did not differ in mNA (TSST: MW = 0.07, SE = 0.02, f-TSST = 0.04, SE = 0.01; $p > .10$).

Positive affect was analyzed with the same ANOVA as negative affect. Positive affect seemed relatively unaffected by the procedures. The ANOVA revealed no significant effects (all $p > .05$).

3.3. Object and face recognition memory

Due to late responses to the object recognition task, 21 out of 3180 possible answers (0.66%) could not be analyzed. A mixed

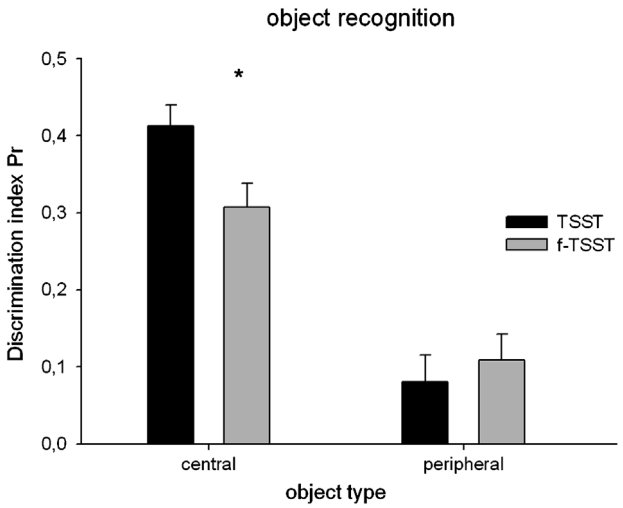

Fig. 2 Object recognition. Memory performance of recognition for central (bound to the stressor) and peripheral objects (not bound to the stressor) of participants exposed to the stress (TSST) or control condition (f-TSST); stressed participants show a better memory performance than control participants in recognizing central objects; the highest possible performance is 1.0; TSST = Trier Social Stress Test; f-TSST = friendly-Trier Social Stress Test; $^{*}p < .05$.

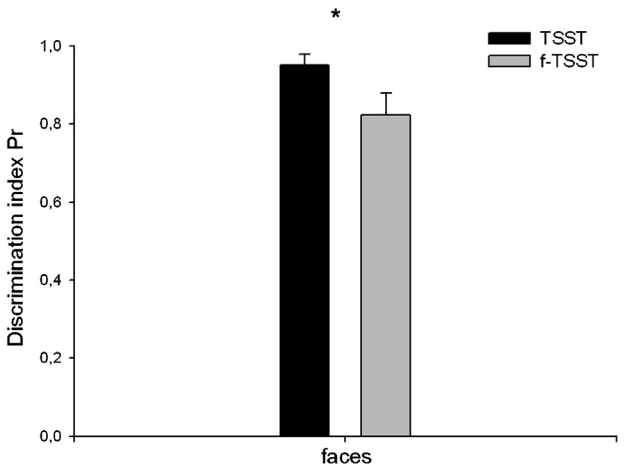

Fig. 3 Face recognition. Memory performance of recognition for the committee's faces of participants exposed to the stress (TSST) or control situation (f-TSST), stressed participants show a better memory performance than control participants in recognizing the committee's faces; the highest possible memory performance is 1.0; TSST = Trier Social Stress Test; f-TSST = friendly-Trier Social Stress Test; $^{*}p < .05$.

model ANOVA for memory performance (Pr) was carried out with OBJECT TYPE (central vs. peripheral) as within-subject factor and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors. We found that stressed participants show better memory performance in recognizing central objects than non-stressed participants (Fig. 2). This was reflected in a significant OBJECT TYPE $\times$ STRESS interaction effect ($F(1,56) = 6.34$, $p = .015$) and a significant main effect of OBJECT TYPE ($F(1,56) = 37.61$, $p < .001$) but no main effect of STRESS ($F(1,56) = 0.88$, $p = .35$). All other effects were not significant ($p > .05$). Planned comparisons as stated in the hypothesis examined the effect of stress on the recognition of central visual details. Analyses confirmed that stressed participants recognize central objects with a significantly better memory performance than non-stressed participants ($t(58) = 2.23$, $p = .03$) with a medium to large effect size Cohen's $d = 0.71$. Unplanned comparisons revealed no group differences for the recognition of peripheral objects ($t(58) = -.58$, $p = .56$). There is a significant difference between object type in both the stress and the control group. Both stressed ($t(29) = 5.54$, $p < .001$) and control participants ($t(29) = 2.79$, $p = .009$) recognized central objects better than peripheral objects (Bonferroni–Holm corrections were applied).

A mixed model ANOVA for HR was carried out with OBJECT TYPE as within-subject factor (central vs. peripheral) and STRESS (stress vs. control) and SEX (male vs. female) as between-subject factors. Results showed a significant interaction OBJECT TYPE $\times$ STRESS ($F(1,56) = 9.40$, $p = .003$) and a significant main effect OBJECT TYPE ($F(1,56) = 30.08$, $p < .001$). Post hoc t-tests showed that stressed participants show a higher HR for central objects than non-stressed participants ($t(58) = 2.73$, $p = .009$), but no differences for peripheral objects($t(58) = -.51$, $p = .615$).

The same ANOVA for FA revealed a significant main effect of OBJECT TYPE ($F(1,56) = 4.19$, $p = .045$) but no further effects (all $p > .05$).

Stressed participants had a better memory for the committee's faces than non-stressed participants ($t(58) = 2.17$, $p = .04$) with a medium effect size of Cohen's $d = 0.56$ (see Fig. 3).

We could not find any significant association between cortisol, sAA, or NA and memory performance.

3.3.1. ROC analyses

A comparable number of data sets from both groups, 6 of the stressed, 4 of the non-stressed group, had to be excluded from group analyses due to an answer level at chance or an inappropriate spread. Data of these participants did not allow the drawing of a ROC curve suitable for analyses because it did not allow a definition of a linear or curvilinear ROC curve.[1]

To test the effect of our manipulation on R and d' in a model-independent manner, data was z-transformed by taking the inverse of the standard cumulative normal distribution of each hit and false alarm rate. Linear and polynomial regressions were fitted to each individual performance and R^2 were compared for polynomial and linear regressions. Paired t-tests on group data (stress vs. control) showed that a polynomial regression resulted in a significantly better fit to the data than a linear regression (TSST: $t(23) = -5.06$, $p < .001$; f-TSST: $t(25) = -6.51$, $p < .001$), suggesting that the best fit for the data samples was a curvilinear function rather than a linear function in z-space. This indicated a linear ROC in normal space. In order to generate a quantitative estimate of recollection on memory performance,

[1] If the same participants are excluded from the memory performance analyses, the reported significant stress effects still persist.

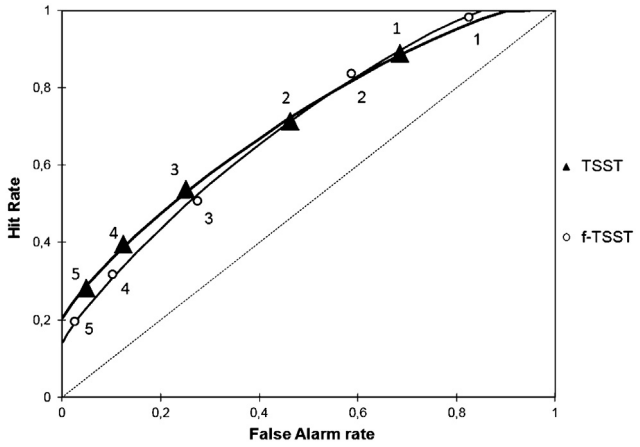

Fig. 4 ROC curves. ROC group curves; stressed participants show a higher *y*-intercept than control participants, there were no group differences in curvilinearity; TSST = Trier Social Stress Test; f-TSST = friendly-Trier Social Stress Test, ROC = Receiver Operating Characteristic; the curve of the TSST group shows a higher *y*-intercept and thus a higher recollection index than the f-TSST group.

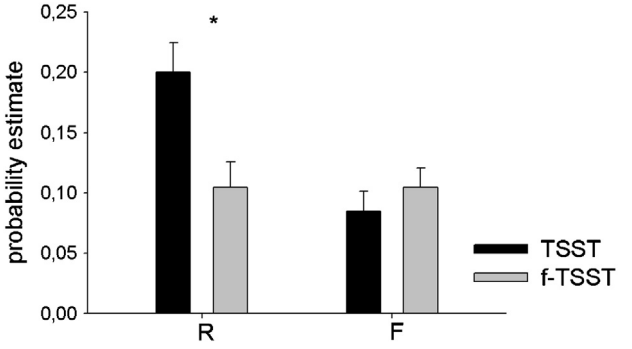

Fig. 5 Recognition memory. Indices of recollection (*R*) and familiarity (*F*) compared between groups; while stressed participants showed a significantly higher recollection value than control participants, there was no group difference in familiarity; TSST = Trier Social Stress Test; f-TSST = friendly-Trier Social Stress Test; TSST participants show a significantly higher *R* index than f-TSST participants; $^{*}p < .01$.

reflected by the *y*-intercept of the ROC curve, and the contribution of familiarity on memory performance, reflected by the degree of curvilinearity of the ROC curve, the dual-process model was used (Yonelinas, 1994). Since model-independent analyses resulted in a linear ROC curve, the model for associative memory was used, because associative memory leads to a linear ROC curve. Memory performance of this model can be described by the following formula: $P(\text{“old”} \mid \text{old}) = R_O + F_O - R_O F_O + P(\text{“yes”} \mid \text{new}) - F_n(1 - R_n)$, where R_O is the probability that an old item is recollected, F_O is the probability that an old item is correctly classified as old by familiarity, F_n is the probability that a new item is wrongly classified as old by familiarity, and R_n is the probability that a new item is correctly recollected as new. ROC curves for each participant were generated by an excel solver using this model with the method of least-squares, and *R* and *d′* were calculated (Yonelinas, 1997). A one-sample *t*-test proved the *y*-intercept to be significantly different from 0 for both groups (TSST: $t(23) = 8.21$, $p < .001$; f-TSST: $t(25) = 4.98$, $p < .001$), proving recollection to be contributing factor to memory performance (see Fig. 4 for grouped ROC curves).

The model-determined parameters of recollection (*R*) in ROC were averaged across groups and compared. Stressed participants showed a higher recollection value than non-stressed participants. This was confirmed by a significant difference for *R* ($t(48) = 2.99$, $p = .004$) in an independent *t*-test between groups with a strong effect of Cohen's $d = .85$. As predicted by the model of associative memory, the values for *d′*, representing a measure of familiarity, were low for both groups. They did not differ significantly between groups ($t(48) = -.81$, $p = .423$). There were no further group differences (all $p > .10$). In order to analyze directly whether stress differentially affects recollection and familiarity, *d′* was transformed into the probability estimate of familiarity (*F*). An ANOVA with PROBABILITY ESTIMATE (*R*, *F*) as within-subject factor and STRESS (TSST vs. f-TSST) as between-subject factor showed a significant PROBABILITY ESTIMATE × STRESS interaction effect ($F(1,48) = 5.92$, $p = .02$) as well as a significant main effect of PROBABILITY ESTIMATE ($F(1,48) = 5.92$, $p = .02$) and of STRESS ($F(1,48) = 6.56$, $p = .01$). A planned comparison confirmed that stressed participants have a higher recollection value than non-stressed participants (see above). Concerning *d′* there was no group difference in *F* ($t(48) = .84$, $p = .40$). See Fig. 5.

ROC analyses for central and peripheral details were not calculated because too many ROC curves showed an irregular shape not suitable for analyses. This might be due to the rather small number of recognition items. Due to practical reasons we were only able to use 8 target items plus the committees' faces and 8 distractor items in the recognition task. Usually, 60 old and 60 new items are used for ROC analyses (Yonelinas and Parks, 2007).

4. Discussion

The current study experimentally investigated memories of a stressful episode in a controlled laboratory setting and compared them with memories of a well-matched control condition. We show that stressed participants have a more accurate memory for central visual details of the episode than non-stressed participants. Moreover, memory performance is predominantly based on recollection.

Social threat causes stress (Dickerson and Kemeny, 2004). During the TSST, stress is caused by the behavior of the committee (Wiemers et al., 2013). Thus the fact that stressed participants have a better memory for the committee's faces appears reasonable. It has been established that activation of the fusiform cortex, which is responsible for processing faces, is modulated by the amygdala, which is in turn activated by emotional arousal (Vuilleumier et al., 2004).

We defined objects as central to the situation if they were interacted with by the committee and as peripheral if they were in the room but left untouched. This definition has been used before (Echterhoff and Wolf, 2012; Peth et al., 2012). In

our study, central visual details of a stressful episode were remembered better than central visual details of a non-stressful situation. This is in accordance with previous eyewitness studies or studies assessing emotional material, which have pointed out an interaction between the relevance (central vs. peripheral) and the emotionality of an item or the emotional state of a person during encoding (Christianson, 1992; Adolphs et al., 2005; Kensinger et al., 2006; Rimmele et al., 2011). The finding that peripheral details are not remembered worse by stressed participants as some hypotheses propose (Easterbrook, 1959; Kensinger, 2009) might be due to the fact that participants engaged in an interaction with the committee during the encoding of the visual objects. It has been shown that a cognitive task during encoding abolishes a trade-off effect between central and peripheral details (Steinmetz and Kensinger, 2013).

There was no difference between groups in memory performance of peripheral visual details, thus there was no obvious trade-off between memory performance for central and peripheral details. This finding fits in perfectly with Mather's object-based framework (Mather, 2007). It suggests that an arousing object evokes focused attention, and that all features of the object are bound together due to the arousal. This process is called within-object binding. Thus, the object as a whole, including its features, is remembered better than a neutral object. Here, we found that arousal does not have to radiate from the item, as is the case with an emotionally loaded picture or word, but that the arousing situation makes an associated object more memorable. Thus, our results extend knowledge from emotional memory research in showing that besides central details of emotional stimuli, neutral stimuli central to a stressful situation will also be remembered better than neutral stimuli central to a non-stressful situation. However, we cannot rule out the possibility that the absence of an effect for peripheral details might partly be due to a floor effect.

As opposed to other studies which presented related material to be learned (Smeets et al., 2007) or unrelated material to be learned (Schwabe and Wolf, 2010) during a stressor, we defined the material to be tested in relation to the committees' actions, the stress causing factor. This could explain why Schwabe and Wolf did not find an enhanced memory performance for material learned during stress. The material may have been too unrelated to the stress inducing factor of the design in order to be central to the situation and thus remembered better. Smeets and colleagues used stressor related material to be learned and could find a memory enhancing effect of stress for stress related material. Thus material to be remembered during stress needs to be related to the stressor or even better central to the stressful situation in the sense we used it here: it has to be strongly related to the stress inducing factor of the particular design.

Our findings suggest that memories of stressful episodes can be traced back to an influence of hippocampal-based recollection memory. This was indicated by a higher recollection value in stressed participants compared to non-stressed ones in ROC analyses. This finding was in line with our hypothesis and fit in with neurobiological models of stress-induced changes in brain function. GCs enter the brain and bind to glucocorticoid receptors in the hippocampus, amygdala and prefrontal regions (de Kloet et al., 1998; McEwen, 2007). Thus, an influence of a hippocampus-based recollection process seems plausible. Previous research on emotions has also shown that memory of arousing and emotional material is influenced to a greater extent by recollection-based retrieval processes. It seems that emotional material, as opposed to neutral material, enhances recollection retrieval (Sharot et al., 2007; Kapucu et al., 2008; Weymar et al., 2010). Familiarity-based recognition memory, which has been linked to parahippocampal areas, appeared not to be influenced by stress in the current study. This is in contrast with two earlier studies showing that familiarity processes are influenced by stress. However, these studies did not assess memories of the stressful episodes, but rather the influence of stress on single item material which was learned previous or concurrent to the stressor, but was not part of or central to the arousing situation itself (Yonelinas et al., 2010; Schwarze et al., 2012).

Our behavioral results fit in with current neurobiological models of stress-induced memory modulations. These have illustrated that stress enhances memory consolidation by activation of the SNS and the HPA axis (Diamond et al., 2005; Joels et al., 2011; Roozendaal and McGaugh, 2011). Underlying mechanisms seem to consist of noradrenergic activity within the amygdala, which leads to a stronger memory for emotionally arousing events (McIntyre et al., 2002). A stress-induced glucocorticoid (GC) signal further potentiates activity in the BLA, which in turn enhances memory storage in the hippocampus (Roozendaal and McGaugh, 2011). The effect of a stronger memory for central items of a stressful episode can thus be most likely traced back to the stress-induced release of noradrenalin and GCs.

Human imaging studies have revealed that during encoding, activation in the amygdala is predictive of emotional memory performance later on (Canli et al., 2000; Dolcos et al., 2004). Furthermore, amygdala activity in response to emotional pictures was especially pronounced in participants exhibiting high endogenous cortisol concentrations. This effect was abolished by betablockers (van Stegeren et al., 2007). Thus, human imaging studies support the notion that an interaction of the SNS and the HPA axis enhances emotional long-term memory via modulatory effects on the amygdala and the adjacent hippocampus.

Rodent studies have illustrated that the event to be remembered and the hormonal changes have to be in temporal and spatial proximity in order to profit from a consolidation-enhancing effect of stress, (Joels et al., 2006). We show that memory for a stressful episode is not globally enhanced; we rather propose that items to be remembered have to be bound to the stressful situation in order to be remembered better. Thus, we propose that activation of the SNS together with the HPA axis leads to a better memory for central visual details of a stressful episode. Rodent studies suggest this to occur in co-activation with the BLA and the hippocampus (Roozendaal and McGaugh, 2011). In order to clarify the possible involvement of these brain regions in humans, imaging studies should examine this hypothesis.

We did not observe any sex differences in the cortisol stress response or in the memory tests. Previous studies have shown that men sometimes show a more pronounced cortisol response to the TSST. In some studies, women show a dampened salivary cortisol response, especially if they use oral contraceptives (Kudielka et al., 2009). However, not all studies show this sex effect (Het et al., 2009). We tested

freely cycling women only, and this might in part explain the missing sex differences. Furthermore, we found no influence of sex on the memory tasks. Only a few previous studies have observed sex differences in the relationship between stress and long-term memory (Wolf, 2011; Andreano et al., 2008). Sex differences might only be apparent at specific stages of the menstrual cycle (Andreano et al., 2008; Schoofs and Wolf, 2009) or in women using oral contraceptives (Kuhlmann and Wolf, 2005; Cornelisse et al., 2011; Merz et al., 2012). Moreover, we recently reviewed evidence that stress might only exert sex-dependent effects on memory tasks in which sex differences already occur without stress (Wolf, 2011). Our current results indicate that memories of a stressful episode do not differ substantially between men and women, at least when both sexes show an equal neuroendocrine response to the stressor.

In sum, our study experimentally demonstrates that central details of a stressful episode are remembered better than those of a non-stressful episode. Moreover, memory traces acquired under stress express themselves in superior recollection memory which is possibly hippocampal-based. Our newly established paradigm and the findings obtained with it should prove valuable for pre-clinical research concerning maladaptive effects caused by strong memories of stressful episodes, as occurring in patients with PTSD.

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Conflict of interest

None declared.

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