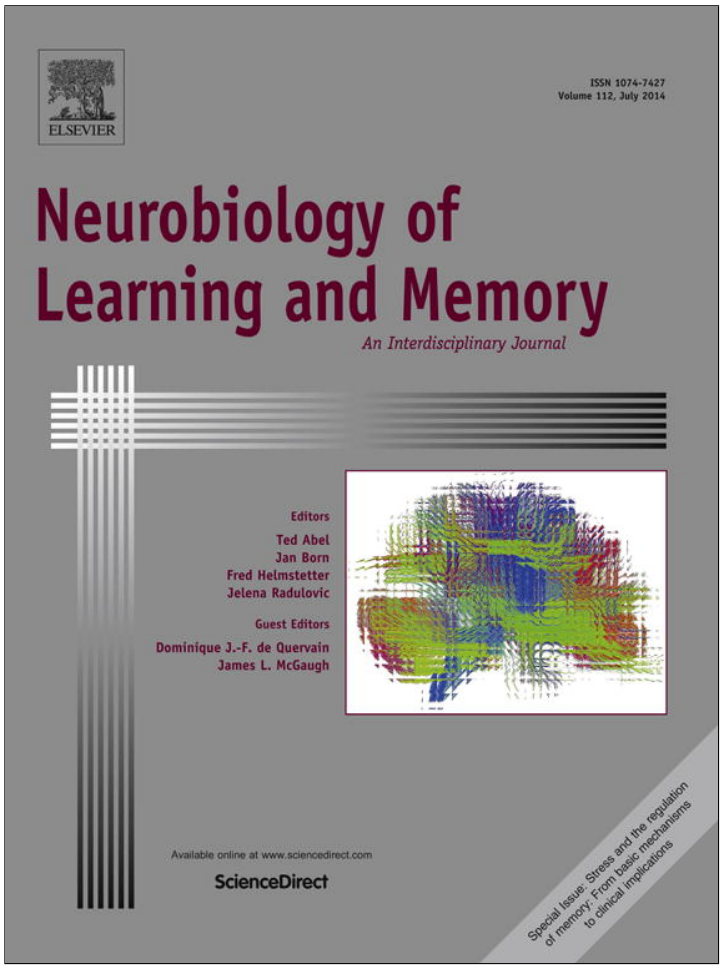

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Odors as effective retrieval cues for stressful episodes

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ABSTRACT

Olfactory information seems to play a special role in memory due to the fast and direct processing of olfactory information in limbic areas like the amygdala and the hippocampus. This has led to the assumption that odors can serve as effective retrieval cues for autobiographic memories, especially emotional memories. The current study sought to investigate whether an olfactory cue can serve as an effective retrieval cue for memories of a stressful episode. A total of 95 participants were exposed to a psychosocial stressor or a well matching but not stressful control condition. During both conditions were visual objects present, either bound to the situation (central objects) or not (peripheral objects). Additionally, an ambient odor was present during both conditions. The next day, participants engaged in an unexpected object recognition task either under the influence of the same odor as was present during encoding (congruent odor) or another odor (non-congruent odor). Results show that stressed participants show a better memory for all objects and especially for central visual objects if recognition took place under influence of the congruent odor. An olfactory cue thus indeed seems to be an effective retrieval cue for stressful memories.

1. Introduction

Processing olfactory stimuli is a unique process in the mammalian brain. Olfactory stimuli are detected by olfactory neurons and are directly transferred to the olfactory bulb and from there directly, without thalamic gating, to the amygdala. The amygdala is directly connected to the hippocampus (Buck, 2000; Mouly & Sullivan, 2010; Wilson, Best, & Sullivan, 2004). Besides being involved in processing of olfactory information, the hippocampus is mainly involved in learning and memory processes, especially episodic memory (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Nadel, Samsonovich, Ryan, & Moscovitch, 2000). The amygdala is mainly involved in the processing of emotional arousal and has a modulating function on memory processes (Cahill & McGaugh, 1998). Thus, by the fast and strong anatomical connection between brain structures processing emotion, memory, and olfactory information it is not surprising that odors appear to play a special role in memory, especially emotional memory processes. It has been shown that memories for odors are very long lasting and do not fade away as memories for e.g. pictures do (Engen, 1987). Furthermore, odors have been found to be effective retrieval cues. Aggelton and Waskett (1999) showed that odor exposure during retrieval enhanced memories for a museum visit where the same odors were present compared to other odors or no odors during retrieval. Odors also enhance context dependent memory when compared to visual cues (Pointer & Bond, 1998). Furthermore memories triggered by odors are older and more emotional than those triggered by verbal cues (Chu & Downes, 2002; Herz & Cupchik, 1995; Willander & Larsson, 2007). Especially odors eliciting memories of aversive events are more detailed, unpleasant, and arousing than memories elicited by verbal cues (Toffolo et al., 2012). When participants are in an anxious and stressed state shortly before an exam, odors can act as effective context retrieval cues which enhance memory (Herz, 1997).

Stress by itself is able to influence learning and memory processes. Stress induces an activation of the hypothalamic–pituitary-adrenal (HPA) axis leading to a release of glucocorticoids (GCs) acting predominately in the hippocampus, the amygdala, and prefrontal regions, all key regions for emotional memory processes (de Kloet, Joels, & Holsboer, 2005; Joels, Karst, DeRijk, & de Kloet, 2008; Ulrich-Lai & Herman, 2009). The direction of stress effects on memory is highly depending on the timing of the stressor. While stress during encoding and consolidation is enhancing memory performance, stress during the time of retrieval has an impairing effect. Additionally, material to-be-remembered has to be associated or bound to the stressor in order to be remembered

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better (Joels, Pu, Wiegert, Oitzl, & Krugers, 2006; Wolf, 2009). Most human studies have investigated effects of stress on memory for material which is often unrelated or only weakly related to the stressor and material was mostly learned shortly after or before stress induction (Schwabe, Bohringer, Chatterjee, & Schachinger, 2008; Smeets et al., 2009). We recently have shown that memory for a stressful episode follows a characteristic pattern itself (Wiemers, Sauvage, Schoofs, Hamacher-Dang, & Wolf, 2013b). We exposed participants either to a psychosocial laboratory stressor (Trier Social Stress Test; TSST) reliably inducing an activation of the HPA axis (Kirschbaum, Pirke, & Hellhammer, 1993) or a newly developed control condition (friendly-TSST; f-TSST) not activating the HPA axis (Wiemers, Schoofs, & Wolf, 2013a). During both conditions participants were exposed to visual objects which were either bound to the stressful situation (central objects) or which were not bound to it (peripheral objects). Consistent with literature from emotional memory research, central visual objects of a stressful episode were remembered better than central visual objects of a non-stressful episode. Furthermore, results from this study (Wiemers et al., 2013b) showed by receiver operating characteristics (ROC) analyses that especially the hippocampal-based retrieval process recollection (Sauvage, Fortin, Owens, Yonelinas, & Eichenbaum, 2008; Yonelinas, 2002) is influenced by stress. The process of familiarity is not influenced by stress. This fits to the dual process model of recognition memory which states that recollection is based on hippocampal processes while familiarity is based on perirhinal processes (Sauvage et al., 2008; Yonelinas, 2002). The effect of stress on only recollection might be attributable to the acting in of GCs in the hippocampus.

The current study sought to investigate whether an odor can serve as effective retrieval cue for memories of a stressful episode. Due to the direct and fast involvement of the amygdala and the hippocampus in olfactory processing and the involvement of exactly those regions in memory enhancing effects due to stress induced hormonal changes, we hypothesized that an odor would serve as especially effective retrieval cue for memories of a stressful episode. We additionally explored the contribution of recollection and familiarity to recognition memory.

2. Methods

2.1. Participants

Ninety-five healthy adults (48 males) between 18 and 32 years of age took part in the experiment. General exclusion criteria were former participation in the TSST, a Body Mass Index (BMI; weight in kg/height in m^2) under 19 or over 30, being in medical treatment, taking medication influencing the HPA axis, and smoking. Pregnant or menstruating women and women taking hormonal contraception were excluded from participation as well, since it has been found that women taking hormonal contraception show a blunted cortisol response to the TSST (Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999). 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 and the Declaration of Helsinki was followed.

2.2. Procedure

On the first day, participants sat in a waiting room, signed informed consent and afterwards performed two tasks irrelevant for current analyses (studying a wordlist and doing a picture story excercise). Fifty-five minutes after arrival participants rated their current affect by filling in the "Positive and Negative Affect Scale" (PANAS, pre; Watson, Clark, & Tellegen, 1988) and delivered the first saliva sample (baseline). Next, participants were brought to a different room where they underwent the stress or control condition, group assignment was random. Stress was induced by a slightly modified version of the TSST, a public speaking task found to reliably induce a cortisol response (Kirschbaum et al., 1993). The friendly-TSST served as non-stressful control condition. It has been shown to not activate the HPA axis (Wiemers et al., 2013a). Both procedures are described more detailed below. During both procedures visual objects and an ambient odor were in the room. After the respective procedure participants were brought back to the waiting room where they delivered the second saliva sample (+1) and filled in the PANAS (post). After 15 min, participants delivered the next saliva sample (+15). The last saliva sample was taken 30 min after the end of the stress or control condition (+30). Afterwards participants were debriefed about the TSST but 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 but this time to a different floor. In a waiting area in the hallway participants first filled in the PANAS and other questionnaires irrelevant for the current report. Next, a saliva sample (day2_pre) was delivered. Then participants were seated into one out of two identical small test rooms which were equipped with a chair, a desk and a PC. In one room the congruent odor (the odor which was present in the TSST/friendly-TSST room the day before) was present in the other room the non-congruent odor was present. This retrieval odor assignment was random. Afterwards participants delivered a last saliva sample (day2_post), did a short anosmia screening, and rated the odor for valence. Finally, participants were thanked, debriefed, and paid.

2.3. Material

2.3.1. Salivary stress markers

Participants were advised 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. Saliva for hormonal assessment was sampled using Salivettes® (Sarstedt, Nuernbrecht, Germany) four times on the first testing day and twice about 24 h later on day 2. Cortisol was analyzed by an immunoassay (IBL, Hamburg, Germany). Inter- and intra-assay variabilities were below 10%. Additionally salivary Alpha Amylase (sAA) was analyzed as an indirect marker for sympathetic nervous system activity as described elsewhere (Rohleder & Nater, 2009). Since cortisol and sAA follow circadian rhythms (Rohleder, Nater, Wolf, Ehlert, & Kirschbaum, 2004; Wolf, Convit, Thorn, & de Leon, 2002) all testing was carried out in the afternoon starting between 1 p.m. and 4.45 p.m. on the first day and starting between 11.30 p.m. and 5 p.m. the second day.

2.3.2. Affect rating

Participants rated current affect on the "Positive and Negative Affect Scale" (PANAS; Watson et al., 1988), a five point scale with 20 items. Items can be subdivided resulting in one value for positive affect (PA) and one for negative affect (NA). We were only interested in changes of negative affect since it has been repeatedly shown that the TSST does not affect positive affect (Schoofs, Preuss, & Wolf, 2008; Wiemers et al., 2013a). Thus, in the following we will only report negative affect. Participants completed the PANAS twice on day 1 and once on day 2.

2.3.3. Stress procedure

2.3.3.1. Tsst. To induce a hormonal stress reaction the Trier Social Stress Test (TSST) was used. It is a standardized psychosocial laboratory stressor leading to a robust activation of the HPA axis (Kirschbaum et al., 1993). Originally, it consists of a 5 min

preparation time, a 5 min free speech about personal characteristics in front of a neutral and reserved acting committee (one male, one female) wearing white coats, and a mental arithmetic task for 5 min. During the latter two tasks participants are videotaped. We used a slightly modified version of the TSST in that we omitted the arithmetic part and instead extended the free speech to 10 min. The omission of the arithmetic part in favor of a longer speech part has been shown to induce a reliable cortisol reaction as well (Wiemers et al., 2013a). The other aspects (behavior of the committee, videotaping) were left unchanged.

Furthermore, the TSST room had been equipped with 20 office objects (e.g. a stapler, a book), which served as recognition objects in a surprise memory recognition task the next day (further details below). Ten of these objects were used by the committee in a standardized fashion.

2.3.3.2. Friendly-TSST. As a well-matched control condition to the TSST the friendly-TSST (f-TSST) was used, which does not trigger a cortisol stress response in the participants (Wiemers et al., 2013a). It consists of the same structure as the modified TSST we applied here: a 5 min preparation time during which participants made notes about their school and university time, career aspirations, hobbies, and favorite book or movie, and a 10 min free speech about life and career aspiration. The committee, wearing white long sleeve shirts instead of white coats in order to avoid an influence of different clothing on attentional processes, reacted friendly by nodding and smiling to give participants a feeling of safety. There was no videotaping during the f-TSST. Since the f-TSST includes the participants' interaction with a committee it ensured that the committee was able to act with the objects the same way as they did in the TSST.

2.3.4. Recognition objects

During the stress or control procedure 20 objects were present in the room. Ten of these were used during the TSST/f-TSST by the committee (pencil, pencil sharpener, stop watch, paper cup, water bottle, toffee tin, stapler, paper tray, eraser, clipboard) and thus bound to the main stressor of the situation (the committee). These objects were thus designated as central objects. Ten objects were not used by the committee and thus not bound to the central stressor of the situation (peripheral objects; puncher, book, file, scissor, handkerchiefs, coffee cup, dustbin, ruler, thumbtacks, and highlighter). Pictures of these objects served as target pictures in a recognition task. Pictures of 40 other objects served as distractor stimuli.

2.3.4.1. Object recognition task. On the second day participants randomly saw pictures of objects on a computer screen for 2 s. After each picture, participants were asked to rate how sure they were whether or not they had seen exactly this object in the TSST/f-TSST room on a 6-point scale ranging from "very sure to have seen the object" to "very sure to not have seen the object", which is important for the ROC analyses (Yonelinas & Parks, 2007). The program only proceeded to the next picture if an answer was given. Preceded by a short blank screen and a fixation cross (1 s. each), the next picture was presented.

2.3.4.2. ROC analyses. ROC curves are defined on the one hand by asymmetry, the height of the y-intercept which indicates a measure of recollection (R; 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 (d′; 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 which points to associative memory processes (Yonelinas, 1997).

2.3.5. Odorants

During the TSST/f-TSST the odorant methyl benzoate was present in the room and thus served as congruent odor. It is an unfamiliar and neutral odor (Sulmont, Issanchou, & Koster, 2002). The odor was dissolved in a concentration of 1.2 ml in 1 l odorless paraffinum liquidum. The odor was distributed by scented cloths hanging on a turning van. Bornyl acetate served as non-congurent stimulus on day 2. It is also an unfamiliar and neutral odor (Sulmont et al., 2002). Odorants were purchased from Sigmar Aldrich, Steinheim, Germany.

3. Results

3.1. Study sample

One male participant was excluded from analyses since he formerly took part in the TSST. Additionally 5 further participants of the control group had to be excluded since they exhibited outlier cortisol values above 2.5 SDs in the Area under the curve with respect to increase (AUCi) measure (Pruessner, Kirschbaum, Meinlschmid, & Hellhammer, 2003), indicating that they showed a cortisol stress response to the control condition. This left 89 participants in the analyses, 46 in the stress group (23 male) and 43 in the control group (20 male). Out of the stress group 22 participants (11 male) did the retrieval task in the odor congruent condition while 24 (12 male) did the task in the odor incongruent condition. Out of the control group 22 (10 male) participants did the retrieval task in the odor congruent condition while 21 (10 male) did the task in the odor incongruent condition. Mean age was 24.12 years and mean BMI of 22.63. There were no differences between the stress or control group in age or BMI (both $p > .10$).

3.2. Stress measures

3.2.1. Cortisol and sAA

Cortisol samples of 73 participants (38 stressed) could be analyzed. The others did not provide enough saliva or contaminated saliva for analyses. Cortisol values were log-transformed since they were not normally distributed. A repeated measures Analysis of Variance (ANOVA) with TIME of cortisol measurements (baseline, +1, +15, +30) as within subject factor and CONDITION (stress vs. control group) and SEX (male vs. female) as between subject factors was conducted.

Stressed participants showed an increase in cortisol concentration as response to the stressor whereas control participants did not (Fig. 1). This was reflected in an interaction effect TIME x CONDITION ($F(3,207) = 27.10$, $p < .001$) as well as a main effect of TIME ($F(3,207) = 14.29$, $p < .001$) and a main effect of CONDITION ($F(1,69) = 12.35$, $p = .001$). There were no effects of SEX (all $p > .10$). Mauchly's test revealed violation of sphericity, thus Greenhouse Geisser corrected p values are reported.

Post-hoc t-tests showed that groups did not differ at baseline ($t(81) = -.98$, $p = .332$) but the stress group showed higher cortisol concentration than the control group 1 min ($t(77) = 2.18$, $p = .032$), 15 min ($t(72.62) = 4.16$, $p < .001$) and 30 min ($t(78) = 4.51$, $p < .001$) after the end of the stressor. Two-sample t-tests showed no group differences in salivary cortisol concentrations on samples provided on the second day, neither for sample day2_pre (stress: M = 0.84, SE = 0.03, control: M = 0.91, SE = 0.04) nor sample day2_post (stress: M = 0.85, SE = 0.04; control: M = 0.88, SE = 0.04; both $p > .10$).

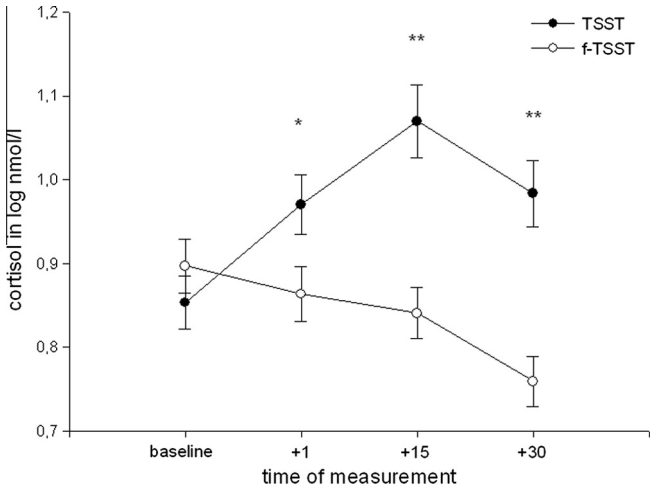

Fig. 1. Salivary cortisol in log nmol/l; cortisol increases as response to the TSST but not to the f-TSST leading to a significant higher cortisol concentration in TSST participants than f-TSST participants at measurement time 1 min (+1), 15 min (+15), and 30 min (+30) after the end of the respective procedure; TSST = Trier Social Stress Test; f-TSST = friendly-TSST; $^{*}p < .05$, $^{**}p < .001$.

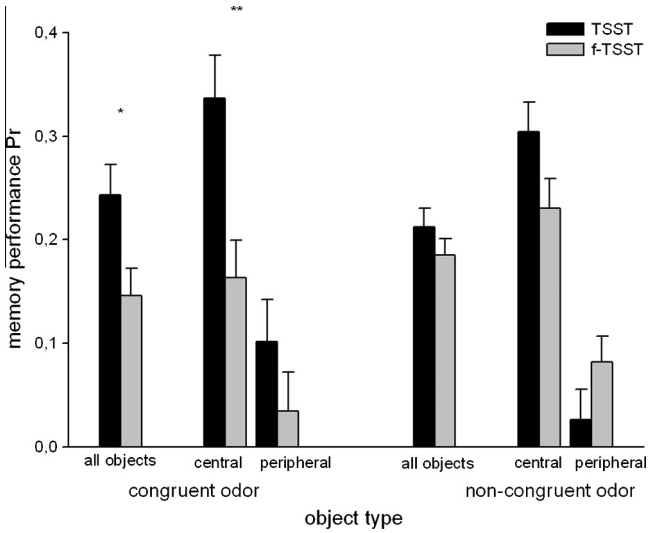

Fig. 2. Memory performance Pr divided into TSST and f-TSST group and into recognition with influence of the congruent odor (methyl benzoate) or the non-congruent odor (bornyl acetate) for all objects, central objects, and peripheral objects; TSST = Trier Social Stress Test; f-TSST = friendly-TSST; $^{*}p < .05$, $^{**}p < .005$.

Results of sAA analyses showed no differences between groups in sAA concentration, TSST as well as f-TSST participants showed a similar increase in sAA concentration in response to the respective procedure (significant main effect of TIME: $F(3,207) = 19.65$, $p < .001$).

3.2.2. Affect results

Values for NA were averaged (mNA) and log-transformed since data was not normally distributed. Repeated measures ANOVA with TIME of measurements (pre, post) as within subject factor and CONDITION (stress vs. control group) and SEX (male vs. female) as between subject factors was conducted.

The TSST and the friendly-TSST had a differential effect on negative affect in the participants. This was validated in the results of the ANOVA. There was an interaction effect TIME x CONDITION ($F(1,83)$=13.483, $p < .001$), a main effect of TIME ($F(1,83) = 2749.56$, $p < .001$), and a main effect of CONDITION ($F(1,83) = 21.63$, $p < .001$). Post-hoc t-tests showed that groups did not differ in NA before the procedure ($t(87) = .84$, $p = .405$) but thereafter ($t(74.69) = 6.61$, $p < .001$, corr.). Stressed participants showed higher negative affect after the procedure (M = 1.24, SE = 0.02) than control participants (M = 1.07, SE = 0.01) but not before the procedure (stress: M = 0.14, SE = 0.02; control: M = 0.11, SE = 0.03). There were no effects of sex. Groups did not differ in NA on day 2 (stress: M = .08, SE = .01; control: M = .06, SE = .02; $p > .10$).

3.3. Object recognition results

Hit rates and false alarm rates were calculated from the object recognition test to obtain a measure of memory performance. Pr was calculated by subtracting the false alarm rate from the hit rate (Snodgrass & Corwin, 1988) for central and peripheral objects. A mixed model ANOVA with OBJECT TYPE (central, peripheral) as within subject factor and CONDITION (stress vs. control group) and SEX (male vs. female) and RECOGNITION ODOR (congruent odor vs. non-congruent odor) as between subject factors was conducted.

Stressed participants in general recognized objects with a higher accuracy than not stressed participants which was reflected in a significant main effect of CONDITION ($F(1,81) = 7.30$, $p = .008$). Furthermore, central and peripheral objects were different accurately recognized. This was reflected in a main effect OBJECT TYPE ($F(1,81) = 72.02$, $p < .001$). Central objects were in general recognized more accurately than peripheral objects. The condition the participants passed through made an influence on how accurately participants recognized the different object types. This was reflected in a significant interaction effect CONDITION × OBJECT TYPE ($F(1,81) = 6.07$, $p = .016$). Stressed participants remembered central objects better than control participants ($t(87) = 3.64$, $p < .001$) but there was no difference in recognizing peripheral objects ($p > .10$).

Most centrally for our hypotheses, the odor exposure during the object recognition task had an influence in combination with the condition the participants ran through (Fig. 2). This was reflected in a significant CONDITION x RECOGNITION ODOR interaction effect ($F(1,81) = 5.55$, $p = .021$). Post- hoc t-tests showed that under the influence of the congruent odor stressed participants were more accurately in recognizing all objects ($t(42) = 2.47$, $p = .018$) as well as central objects ($t(42) = 3.19$, $p = .003$) than not stressed participants, while there was no difference between groups in recognizing peripheral objects. Under the influence of the non-congruent odor there were no significant group differences in recognizing the objects (all $p > .05$). There were no effects of sex (all $p > .10$)

If results were split into stress and control group there were no significant differences in object recognition performance between the congruent and incongruent odor retrieval groups ($p > .10$).

3.4. ROC results

To determine the contribution of recollection and familiarity on recognition memory ROC analyses were performed (Yonelinas & Parks, 2007). We generated ROC curves for each individual by plotting the probability of hits against the probability of false alarms across five cumulated bias levels (Yonelinas & Parks, 2007) analogous to analyses in Wiemers et al., 2013b. For further analyses we included 76 (42 stress) participants, the others were excluded due to an answer level at chance or an inappropriate spread which made generation of a ROC curve impossible.[1] In order to examine the influence of stress on recollection and familiarity in a model

[1] If the same participants were excluded from the accuracy analyses the reported significant effects still exist.

independent manner data was *z*-transformed by taking the inverse of the standard cumulative distribution of each hit and false alarm rate. Linear and polynomial regressions were fitted to the data for each individual. R^2 were compared showing that polynomial regression resulted in a significantly better fit to the data than linear regression (stress: $t(41) = -6.94$, $p < .001$ control: $t(33) = -6.38$, $p < .001$). Thus a curvilinear fit in z-space fitted the data best, resulting in a best linear fit in normal space. These results show that the contribution of familiarity to recognition memory, which is reflected by the degree of curvilinearity, is negligible here and this points to associative memory (Yonelinas, 1997). Thus an excel solver for associative memory was used in order to generate ROC curves for each participant (Yonelinas, 1997). In this model the *y*-intercept of the curve (R) provides a measure for recollection, the degree of curvilinearity (d′) a measure for familiarity. Mean values were calculated for R and d′.

A univariate ANOVA was calculated with R as dependent variable and CONDITION (stress vs. control group) and RECOGNITION ODOR (target odor vs. distractor odor) as independent variable. Results show a significant main effect of condition ($F(1,72) = 4.16$, $p = .045$). Stressed participants show a higher recollection value (M = 0.13, SE = 0.02) than not stressed participants (M = 0.08, SE = 0.01) replicating earlier results (Wiemers et al., 2013b). Post-hoc two sample t-tests confirmed that result. The stressed group showed a trend towards a higher value of R than the control group ($t(74) = 1.96$, $p = .053$). Furthermore we split participants into two odor groups (congruent vs. non- congruent). Independent t-tests showed that under the influence of the target odor stressed participants showed a higher recollection value (M = 0.13, SE = 0.03) than control participants (M = 0.06, SE = 0.02; $t(29.22) = 2.04$, $p = .05$, corr.). There were no significant group differences under the influence of the distractor odor ($p > .10$). The same ANOVA for d′ resulted in no significant effects (all $p > .10$) indicating that familiarity was neither influenced by stress nor by the odor conditions.

3.5. Odor ratings

In order to assess the valence ratings of the participants we split the group into stress and control group and used paired t-tests assessing whether valence of methyl benzoate was different from bornyl acetate and found that in the control group there was no difference in valence ($p > .10$). In the stress group there was a difference in valence ($t(45) = 2.54$, $p = .015$). Stressed participants rated the congruent odor slightly more unpleasant than the non-congruent odor.

Furthermore we found with two-sample *t*-tests that valence neither for the target odor methyl benzoate ($t(87) = 1.55$, $p = .13$) nor for the distractor odor bornyl acetate ($t(87) = 1.02$, $p = .31$) differed between stress and control group.

4. Discussion

The current study sought to investigate the influence of an odor as context cue for memories of a stressful episode. As expected, participants showed an activation of the HPA axis in response to the stressor. This was visible in a significant increase in cortisol after the TSST. In contrast, participants exposed to the friendly-TSST showed no increase in cortisol thus there was no HPA axis activation in response to the control condition. Participants showed in general enhanced memory performance for central details compared to peripheral details. Importantly we could replicate our recent results in showing that stressed participants display enhanced recognition performance for central visual details compared to not stressed control participants (Wiemers et al., 2013b). This fits well into current research since many theories propose that central details will be remembered better than peripheral details (Easterbrook, 1959; Kensinger, 2009; Mather, 2007; Waring & Kensinger, 2011) especially if encountered during emotional arousal and under stress (Wiemers et al., 2013b).

In line with our hypothesis we could show that an olfactory retrieval cue is especially effective in cueing memories of a stressful episode compared to a non-stressful episode. This is in line with previous studies which showed that an odor is an effective retrieval cue (Aggleton & Waskett, 1999), especially if participants are in an anxious and aroused state during encoding (Herz, 1997). The non-congruent odor however did not lead to a difference in recognition between stress and control group and also there were no differences in object recognition performance between the retrieval conditions within the stress and control group. Thus, only stress in combination with the congruent odor as memory retrieval cue led to an enhanced memory performance compared to the control group.

As limiting factor could be seen the fact, that the same odor was used as target odor for all participants. However, since TSST and f-TSST were conducted in the same room, we decided to always use the same odor as target odor in order to prevent a carry-over effect of smells from one participant to another.

In the first study from us on this topic (Wiemers et al., 2013b) memory testing was performed in a familiar room (the room where participants waited and performed tasks before and after the TSST/f-TSST). Thus in the first study a contextual (visual-spatial) retrieval cue was present. In the current study testing on day two took place in an unfamiliar testing room located at a different floor in our department. Thus, only in the congruent odor condition a contextual (olfactory) cue was present. Trying to integrate the findings from our two studies we speculate that the stress associated memory enhancement of central visual details in our paradigm can only be detected in the presence of some contextual retrieval cues (spatial or olfactory). Previous studies testing the impact of stress on memory consolidation have typically not varied the retrieval context systematically and the procedural descriptions are often not detailed enough in order to evaluate the presence or absence of contextual retrieval cues.

Our memory task is rather difficult since it relies on the implicit encoding of every day office items. Moreover the used distractors are in part highly similar to the targets. Thus the task is rather difficult. It is conceivable that effects of stress on the long-term memory consolidation of more distinct or more arousing stimuli is more pronounced and less dependent of contextual retrieval cues.

The effect we found here cannot be ascribed to different valence of the odors. Control participants rated target and distractor odor similar in valence. The difference in valence ratings of the two odors in the stress group most probably can be ascribed to the encountering of the odor in an unpleasant stressful condition. Also familiarity of the odors is supposed to be equal (Sulmont et al., 2002) even though we did not assess this aspect in the current study. Arousal ratings of the odors are missing and should be conducted in future studies.

The memory enhancing effect we found here goes nicely with the model proposed by Joels and colleagues which states that in order to enhance memory stress must be present at the time of encoding or consolidation, material to be remembered must be bound to the stressor, and stress hormones must be acting in the same areas as arousing hormones (Joels et al., 2006). This is the case in the current study. Furthermore, amygdala and hippocampus, primary targets for modulating stress induced hormonal changes on memory processes (especially memories for emotionally arousing situations; Baddeley, 2001; Cahill & McGaugh, 1998; Joels et al., 2006; Ulrich-Lai & Herman, 2009) are also heavily involved in processing olfactory information (Buck, 2000; Mouly &

Sullivan, 2010). An olfactory cue present at the time of stress thus activates the same areas which are activated due to stress: hippocampus and amygdala. Thus activation due to stress and the olfactory cue might strengthen the association between the central aspects of a stressful episode and the olfactory information. This association might be consolidated together and at retrieval the olfactory context-cue is able to access memories for the central aspects of the stressful episode, leading to an enhanced memory performance for them.

Context-dependent memory, meaning the dependency of the encoding process on the retrieval process (Tulving & Thomson, 1973), has been studied frequently. It states that a congruency between encoding and retrieval of information leads to a better memory performance. Environmental context effects denote enhanced memory performance if learning and retrieval take place in the same environment (Smith & Vela, 2001). Godden and Baddeley (1975) showed, for example, that scuba divers recalled more words if learning and retrieval both took place on land or both in water compared to mismatching environments at learning and retrieval. The context effect is ascribed to the assumption that environmental cues are incidentally encoded together with the material to be remembered (Moscovitch et al., 2005). In the current study the odor was also incidentally encoded with the stressful episode and thus can be seen as environmental retrieval cue.

Our results seem at first glance contradictory to former studies which found that stress abolishes the context dependent memory effect (Schwabe, Bohringer, and Wolf (2009), Thompson, Williams, L'Esperance, and Cornelius (2001)). However, Schwabe et al. assessed the effectiveness of a context-cue on a spatial memory task learned shortly after stress induction and not memories of a stressful episode, as we did. It seems plausible that items which are associated to the stressor are encoded preferentially and memory of those items is therefore enhanced opposed to those items which are not related to the stressor. The material used in the former mentioned study most likely was not bound to or central to the stressor. Thus even though a context effect for material unrelated to the stressor might vanish if stress is induced shortly before encoding (Schwabe, Bohringer, & Wolf, 2009) an odor as context dependent retrieval cue might enhance memories for central aspects of the stressor if the odor is present during the stressor itself. Thompson, Williams, L'Esperance, and Cornelius (2001) used skydiving (learning and encoding in the air or on land) as context cue, while sky diving of course was also stressful itself. Results show that the context-dependent enhancement of memory was only present for learning and retrieval on land but not during skydiving. This could be due to probably high cortisol concentrations during encoding as well as during retrieval since stress at retrieval is thought to impair memory (Buchanan & Tranel, 2008; de Quervain, Roozendaal, Nitsch, McGaugh, & Hock, 2000; Kuhlmann, Kirschbaum, & Wolf, 2005a; Kuhlmann, Piel, & Wolf, 2005b; Smeets, Otgaar, Candel, & Wolf, 2008; Tollenaar, Elzinga, Spinhoven, & Everaerd, 2008). Thus a worse memory performance during the skydiving condition at retrieval seems plausible. We stressed participants only during encoding but not during retrieval thereby inducing an enhancing effect of stress and thereof resulting hormonal changes on memory encoding and consolidation (Cahill, Gorski, & Le, 2003; Diamond, Park, Campbell, & Woodson, 2005; Joels et al., 2006; Kuhlmann & Wolf, 2006; Preuss & Wolf, 2009; Roozendaal & McGaugh, 2011; Sandi & Pinelo-Nava, 2007; Smeets et al., 2008).

Our results fit also well to findings with PTSD patients. Combat veterans with a current PTSD diagnosis rated diesel smell, an olfactory reminder of combat, as more distressing and unpleasant than combat veterans without a PTSD diagnosis. Furthermore the patients' symptoms were increasing as result of the smell exposure. Thus olfactory cues appear to be strong reminders of distressing situations (Vermetten, Schmahl, Southwick, & Bremner, 2007).

Analogous to a former study (Wiemers et al., 2013b), current results show an influence of stress on the hippocampal based recollection process in that stressed participants show higher recollection retrieval than not stressed participants. Familiarity was not influenced by stress. This might reflect GCs acting in the hippocampus. Here we extend findings in showing that in a congruent odor condition at encoding and retrieval recollection retrieval was more pronounced in the stress than in the control group while the incongruent condition abolished this effect.

In sum, with the current study we were able to replicate results from a previous study (Wiemers et al., 2013b) in showing that stressed participants show a better memory for central details of a stressful episode compared to not stressed participants and stress primarily influences recollection. We furthermore were able to extend these findings in showing that an olfactory stimulus is a potent retrieval cue for memories of the stressful episode. We ascribe this to a concurrent activation of brain regions due to stress and the olfactory information processing during encoding which leads in combination with the action of GCs in these areas to a better consolidation of visual details which are bound to the stressful situation together with the odor. The same olfactory cue at retrieval leads to an enhanced memory performance for the visual material. Our findings support the notion that olfactory cues are especially well suited to trigger emotional memory retrieval.

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