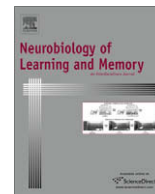




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Post-learning psychosocial stress enhances consolidation of neutral stimuli

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ABSTRACT

Post-learning stress has been reported to enhance memory consolidation in humans. This effect was observed in studies using physical stressors or an anticipatory speech task. In the present study 58 participants (28 females and 30 males) were exposed to a psychosocial stressor (Trier Social Stress Test) or a control condition following the presentation of neutral and emotionally arousing positive and negative pictures, which were accompanied by a brief narrative. The stressor induced a significant neuroendocrine stress response in men and women. In a 24 h delayed free recall test the stress group showed an enhanced memory for neutral but not for emotionally arousing positive and negative items. Additionally, a significant correlation between the cortisol stress response and memory for neutral items was evident. Thus, in contrast to previous studies, post-learning stress primarily enhanced consolidation of neutral material. Several theoretical and methodological explanations for the observed effects are discussed.

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1. Introduction

We know from everyday experiences that stressful events are well remembered and experimental laboratory research has shown that stress influences memory (Wolf, 2008). The modulatory effects of stress on memory are caused by the release of stress hormones. The activation of the sympathetic nervous system (SNS) in response to stress results in a release of catecholamines. Additionally, the hypothalamic-pituitary (HPA) axis is activated, which results in the release of glucocorticoids (GCs; de Kloet, Joels, & Holsboer, 2005).

The effects of stress on memory depend on the particular memory phase influenced by stress (Roosendaal, Okuda, de Quervain, & McGaugh, 2006; Wolf, 2008). Additionally, it became apparent that stress differs depending on whether it is related to the learning situation or is outside the learning context (Joels, Pu, Wiegert, Oitzl, & Krugers, 2006). Increasing the stressfulness of a learning episode was found to enhance memory in rodents (Akirav et al., 2004; Akirav, Sandi, & Richter-Levin, 2001; Sandi, Loscertales, & Guaza, 1997). Akirav et al. (2004) for example observed that rats performed better in a spatial task (Morris Water Maze) when the situation was so designed as to be more stressful (colder water temperature). The authors could demonstrate that this memory enhancement was due to the release of corticosterone. Similarly, glucocorticoids injected immediately after acquisition (post-learning)

and thereby influencing memory consolidation were found to enhance consolidation of newly learned material (Roosendaal, de Quervain, Ferry, Setlow, & McGaugh, 2001; Roosendaal, Nguyen, Power, & McGaugh, 1999).

The empirical picture becomes more complex when stressor and learning task are not directly associated and the stressor is detached from the learning episode. This is the case when the animal receives foot shocks or is exposed to a predator before or after learning a maze task (e.g. Park, Zoladz, Conrad, Fleshner, & Diamond, 2008).

Similarly, in human studies, the stressor (e.g. cold water immersion or a public speech) is typically unrelated to the memory tests conducted (e.g. Beckner, Tucker, Delville, & Mohr, 2006; Cahill, Gorski, & Le, 2003; Wolf, Schommer, Hellhammer, McEwen, & Kirschbaum, 2001). When reviewing previous human studies using this approach pre-learning and post-learning stress exposure need to be differentiated.

With respect to pre-learning stress, enhancing as well as impairing effects have been observed. The direction of the effects appears to depend on several variables. The delay between stress exposure and the learning episode (Diamond, Campbell, Park, Halonen, & Zoladz, 2007) and the delay between initial learning and recall (immediate vs. delayed recall; Elzinga, Bakker, & Bremner, 2005) have turned out to be important variables. Moreover the emotionality of the learning material has been reported to influence the outcome in that, although pre-learning stress impaired neutral memory, it often enhanced emotional memory (Jelici, Geraerts, Merckelbach, & Guerrieri, 2004; Payne, Jackson, Hoscheidt, Ryan, Jacobs, et al., 2007; Schwabe, Bohringer, Chatterjee, & Schachinger, 2008).

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For post-learning stress exposure, the empirical picture is more homogenous and reveals mostly enhancing effects. Several human studies observed that immediate post-learning stress either with the cold pressure test (CPT; Andreano & Cahill, 2006; Cahill et al., 2003; Smeets, Otgaar, Candel, Wolf, 2008) or with an anticipatory speech stressor (Beckner et al., 2006) led to enhanced memory consolidation. In those studies which used negative as well as neutral learning material, the effect was only found for the emotionally arousing negative items (Cahill et al., 2003; Smeets, Otgaar, Candel, & Wolf, 2008). In line with these stress studies we recently reported that basal cortisol levels were specifically associated with enhanced memory for emotional items (Preuss, Schoofs, Wolf, & emotional memory: influence of encoding instructions. *Stress*, in press). However, the beneficial effects of post-learning stress on memory consolidation have also been reported in studies where only neutral learning material was employed (Andreano & Cahill, 2006; Beckner et al., 2006).

An impact of sex on the relationship between stress and memory has been reported in previous research. One aspect is that the HPA stress response to performance based laboratory stressors is influenced by sex. Men often show a more salient response than women (Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999; Kirschbaum, Wust, & Hellhammer, 1992; Stroud, Salovey, & Epel, 2002) but contrary results have also been reported (Kelly, Tyrka, Anderson, Price, & Carpenter, 2008). Additionally there are not only sex differences in the HPA reactivity to psychosocial stress but also sex differences for the influence of stress on memory or emotional learning. The effects of GCs here were repeatedly found to be more pronounced for men than for women (Andreano & Cahill, 2006; Cahill, 2003; Jackson, Payne, Nadel, & Jacobs, 2006; Stark, Wolf, Tabbert, Kagerer, Zimmermann, et al., 2006; Wolf et al., 2001; Zorawski, Blanding, Kuhn, & LaBar, 2006). Possible sex differences should therefore be considered when exploring the influence of stress on memory (Cahill, 2006; Wolf, 2008).

Building up on recent findings in the field the present study was conducted to further clarify the influence of stress on consolidation. Existing studies evaluating the influence of stress on consolidation processes have either used a physical stressor (Andreano & Cahill, 2006; Cahill et al., 2003; Smeets et al., 2008) or an anticipatory speech stressor where the speech itself had not to be performed (Beckner et al., 2006). To date, no experiment has systematically assessed the influence of the Trier Social Stress Test (TSST, Kirschbaum, Pirke, & Hellhammer, 1993) on memory consolidation. This stressor typically leads to a more pronounced cortisol stress response compared to the CPS or anticipatory speech stressors used in previous consolidation studies (Beckner et al., 2006; Cahill et al., 2003; Kirschbaum et al., 1993; Kuhlmann, Piel, & Wolf, 2005; van Stegeren, Wolf, & Kindt, 2008). In addition it has a stronger 'cognitive load', since the subjects have to deliver a speech and work on a mathematical task. The aim of the present study was to evaluate the effects of post-learning stress on memory consolidation. Based on previous observations, as summarized above, the factors emotional arousal of the learning material as well as sex of the participants was taken into account.

2. Materials and methods

2.1. Participants

Participants were 30 healthy men and 30 healthy free cycling women. Women were tested during the whole menstrual cycle except menses. Two outliers with data above or below 2, 5 standard deviations in immediate memory recall scores had to be

excluded and the data of 58 participants (28 female, 30 male) was analyzed. Women were between the age of 19 and 28 (mean age 23.68 ± 0.45). Men were between the age of 20 and 29 (mean age 23.53 ± 0.48). Mean body mass index for the men was $24.12 (\pm 0.45)$ and for the women $21.56 (\pm 0.49)$. Participants were excluded if they reported any use of medicaments that could have influenced the hormonal stress response (e.g. antibiotics, and antihistamines). Women were free of hormonal contraception. All participants were recruited at the university campus and written informed consent was collected from each subject. The study was approved by the national ethic committee of the German Psychological Association (Deutsche Gesellschaft für Psychologie).

2.2. Materials

2.2.1. Stimuli

The stimuli and memory tests used in the present study were developed and validated by Buchanan, Karafin, and Adolphs (2003). The material, recently translated by our group, had been used in a first study testing the associations between basal cortisol levels and emotional memory (Preuss et al., in press). The stimuli consisted of five positive (e.g. two happy girls eating ice-cream), five negative (e.g. a diseased child from Africa with bandages and cannulae) and five neutral (e.g. people leaving or entering a building) pictures, each presented in a random order for a duration of 10 sec on a computer screen. Several of these pictures were chosen from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1997) and the remaining drawn from print media sources. Each picture was accompanied by a single narrative sentence which consisted information that was not obvious in the picture. For example the picture with the little girls eating ice-cream was accompanied by a sentence in which the girls' names and the special kind of ice-cream they preferred being mentioned.

2.2.2. Memory tasks

Participants solved several written memory tests.

2.2.3. Immediate recall test

The immediate free recall test took place immediately after the presentation of the pictures. Participants were asked to write down everything they remembered from the pictures and narratives. Time was restricted to 5 min. Answers were evaluated by two independent judges. Differences in test scores were discussed and were solved by a third judge. A participant received three points, if the information noted could be clearly associated to one of the pictures and was correct in details. Two points were given for information that could be clearly associated to one of the pictures but consisted of some wrong details. If the information was completely wrong or could not be linked to one picture, participants got one point. A total of 45 points could be achieved.

2.2.4. Delayed recall test

On the second day, 24 h after presentation of the pictures, the delayed free recall test was conducted. Again, participants were given 5 min to write down everything they remembered from the pictures and narratives. Answers were evaluated in the same manner as in the immediate recall test.

2.2.5. Multiple choice test

This task consisted of six questions asking for information pertaining to pictures and narratives for each stimulus. In this task every correct answer scored a point, so that a total of 90 points was possible.

2.2.6. Memory for gist and detail

The multiple choice test also permits a differentiation between memory for gist and detail information. Gist is defined as “an information which could not be changed or excluded without changing the basic story line” (Heuer & Reisberg, 1990). According to Buchanan et al. (2003) 47 questions referred to gist information and 37 to detail information. The remaining six items could not be categorized clearly and were thus not included in the gist analysis (Buchanan et al., 2003). Here again every correct answer scored one point, so that 47 points for the gist items and 37 points for detail items were achievable. In order to allow comparisons between memory for gist and memory for detail memory performance was expressed in percentages.

2.2.7. Mood assessment

2.2.7.1. Positive and negative affective schedule (PANAS; Watson, Clark, and Tellegen, 1988). This questionnaire consists of ten items for negative and ten items for positive mood. For the present study, only the negative mood scale was used. Participants filled out the PANAS three times, the first time before the presentation of the pictures, the second time after the stress or control condition and for the third time at the beginning of the memory tests on the second day.

2.2.8. Stressor and control condition

In the present study a psychosocial stressor, the Trier Social Stress Test (TSST; Kirschbaum et al., 1993), was used. This stress protocol consisted of a video-taped oral presentation and an arithmetic task before a panel (one woman and one man) whose attitude was very reserved. This psychosocial stressor, with a total duration of 15 min, reliably elicits a response of the HPA and SNS (Dickerson & Kemeny, 2004; Kuhlmann et al., 2005). The non-stressful control condition also consists of an oral presentation and an arithmetic task but participants did not perform in front of an audience and were not video-taped. The control condition therefore lacks the stressful components of the TSST and did not elicit a cortisol stress response (Dickerson & Kemeny, 2004; Kuhlmann et al., 2005).

2.2.9. Saliva samples

Saliva was collected using Salivette collection devices (Sarstedt, Nümbrecht, Germany). Totally, seven saliva samples were collected, five on the first day and two on the second day. Cortisol (Kirschbaum & Hellhammer, 1989) and Alpha-Amylase (sAA) as a measure of SNS activity (Chatterton, Vogelsohn, Lu, Ellman, & Hudgens, 1996; Rohleder, Nater, Wolf, Ehler, & Kirschbaum, 2004; van Stegeren, Rohleder, Everaerd, & Wolf, 2006) were assessed.

2.3. Procedure

The experimental protocol is illustrated in Fig. 1. Participants were tested on 2 days 24 h apart. The testing started between

2 p.m. and 4 p.m. After arrival on the first day, participants filled out the PANAS for the first time (PANAS pre-treatment). Subsequently, the first saliva sample was collected (base 1), followed by presentation of the pictures and narratives. Participants then solved the immediate recall test and collected the second saliva sample (base 2) after finishing the test. This was followed by the TSST or the control condition. Only after entering the TSST or control condition room were participants aware of whether or not they would be part of the stress or control condition. Afterwards the third saliva sample was collected (+01) and subjects filled out the PANAS for the second time (PANAS post-treatment). Then the fourth saliva sample was assessed (+10). The last saliva sample (+25) on the first day was collected 25 min after the respective treatment. Participants were debriefed about the TSST at the end of the first day. On the next day, 24 h after the encoding of the pictures on the first day, participants returned to the laboratory and the first saliva sample (pre) was collected before they filled out the PANAS for the third time (PANAS day 2). Subsequently, they solved the memory tests and the last saliva sample (post; approximately 45 min after the first saliva sample) was collected.

2.4. Statistical analyzes

Data were analyzed with *t*-tests or ANOVAs for repeated measurements and post-hoc paired *t*-tests. Greenhouse–Geisser corrected *p* values were used when indicated. Cortisol baseline levels were normally distributed. Because saliva alpha-amylase baseline measure did not show a normal distribution, data were log 10 transformed to approximate them to Gaussian distribution. After transformation all data were normally distributed.

3. Results

3.1. Cortisol response

The cortisol responses to the TSST for the entire sample, as well as for women and men separately, are displayed in Fig. 2. To analyze the cortisol response an ANOVA with the inner subject factor time (base 1 vs. base 2 vs. +01 vs. +10 vs. +25) and the between subject factors stress (TSST vs. control condition) and sex (male vs. female) was conducted.

A main effect of time occurred ($F(4, 216) = 8.990, p < 0.01$). Additionally, main effects for sex ($F(1, 54) = 8.429, p < 0.05$) and stress occurred ($F(1, 54) = 21.111, p < 0.001$). Also the interactions between time and stress ($F(4, 216) = 27.990, p < 0.001$) reached significance. The interaction between sex and stress ($F(4, 216) = 3.483, p = 0.05$), sex and time ($F(4, 216) = 3.483, p = 0.05$) and sex and stress and time ($F(4, 216) = 3.464, p = 0.05$) just fell short of significance. For further evaluation *t*-tests were conducted for the comparison between the conditions and additionally for the sexes. The TSST group had higher cortisol levels for the measurements +01 ($t(56) = -4.534, p < 0.001$), +10 ($t(56) = -5.565, p < 0.001$) and +25 ($t(56) = -5.388, p < 0.001$).

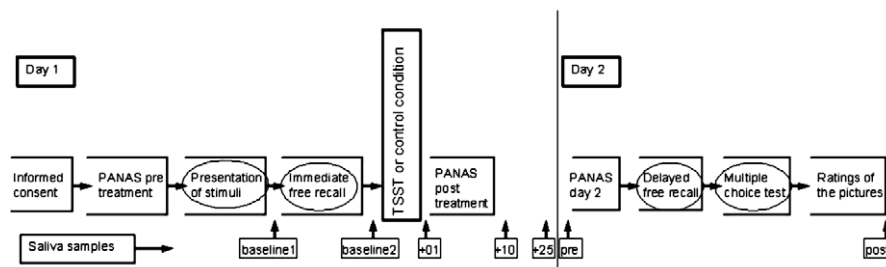


Fig. 1. Procedure of the study.

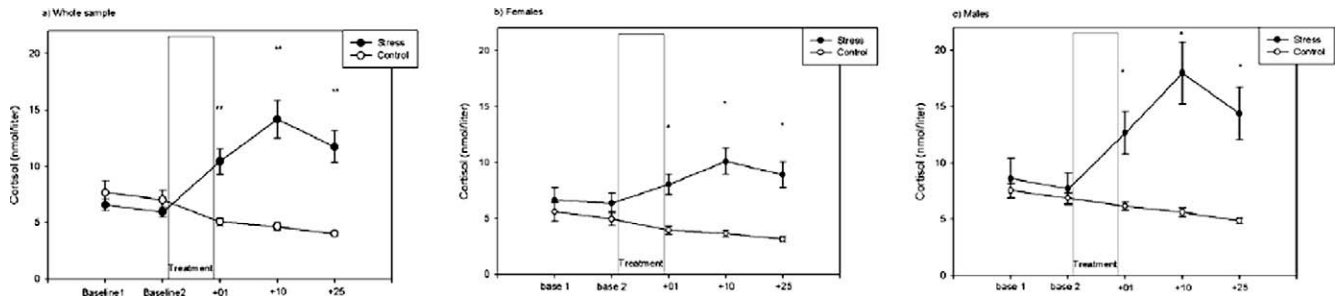


Fig. 2. Cortisol response to the TSST and the control condition. A significant interaction between stress and time occurred in the ANOVA. Follow-up *t*-tests revealed significant differences between TSST and control group for (a) the whole sample, (b) females and (c) males at measurements +01, +10 and +25 (** $p < 0.001$; * $p < 0.05$).

No difference was observed for the remaining measurements (all $p > 0.10$). Post-hoc *t*-test for the comparison between males and females were conducted for the baseline measurements and the rise in cortisol (measurement +10 – baseline measurement) in response to the TSST. No difference was found for the baseline measurements (all $p > 0.05$). For women, a rise in cortisol (measurement +10 – baseline measurement) of 3.76 nmol/l (± 1.66) was detected while cortisol levels in men showed a significantly stronger rise of 10.72 nmol/l (± 2.16 ; $t(27) = -2.369$, $p < 0.05$). Additionally, *t*-tests were conducted for the two sexes separately. For both sexes higher cortisol values were found for the TSST group for the measurements +01 (males: $t(28) = -3.404$, $p < 0.01$; females: $t(26) = -4.233$, $p < 0.001$), +10 (males: $t(28) = -4.424$, $p < 0.001$; females: $t(26) = -5.443$, $p < 0.001$) and +25 (males: $t(28) = -4.057$, $p < 0.001$; females: $t(26) = -4.760$, $p < 0.001$) but not for the remaining time points (all $p > 0.05$).

For the second day, an ANOVA with the inner subject factor time (pre- vs. post-) and the between subject factors stress (TSST vs. control condition) and sex (male vs. female) was conducted. Results revealed a main effect of time ($F(1, 54) = 31.913$, $p < 0.001$) and sex ($F(1, 54) = 7.022$, $p < 0.001$). The remaining effects did not reach significance (all $p > 0.05$). To assess the significant main effects of time and sex further, additional *t*-tests were conducted. Results revealed that males had higher cortisol levels than women at both measurements (pre: $t(56) = 2.330$, $p < 0.05$; post: $t(56) = 2.975$, $p < 0.01$). Analysis of the significant main effect of time showed that cortisol levels on the second day decreased slightly but significantly during testing ($t(57) = 5.746$, $p < 0.001$) from 6.25 (± 0.45) to 4.58 (± 0.24) nmol/l (males: from 7.24 (± 0.66) to 5.22 (± 0.34) nmol/l; females: from 5.21 (± 0.56) to 3.90 (± 0.30) nmol/l) reflecting the well known circadian decline of the hormone.

3.2. Alpha-amylase response (sAA)

The sAA responses to the TSST for the entire sample as well as for women and men are separately displayed in Fig. 3. To analyze

the sAA stress response an ANOVA with the inner subject factor time (base 1 vs. base 2 vs. +01 vs. +10 vs. +25) and the between subject factors stress (TSST vs. control condition) and sex (male vs. female) was conducted.

The main effects of time ($F(4, 204) = 27.639$, $p < 0.001$) and stress ($F(1, 54) = 5.530$, $p < 0.05$) were significant. Additionally, a significant interaction effect between time and stress occurred ($F(4, 204) = 4.573$, $p < 0.05$). The remaining effects did not reach significance (all $p > 0.10$). Post-hoc *t*-test revealed higher values in the TSST group at measurements +01 ($t(56) = -3.826$, $p < 0.001$), +10 ($t(56) = -2.555$, $p < 0.05$) and +25 ($t(56) = -2.101$, $p < 0.05$) but not at the other measurements (all $p > 0.10$).

For the second day an ANOVA with the inner subject factor time (pre vs. post) and the between subject factors stress (TSST vs. control condition) and sex (male vs. female) was conducted. No significant results were detected (all $p > 0.05$).

3.3. Mood

To evaluate changes in mood in reaction to the TSST an ANOVA with the factors time (pre-treatment vs. post-treatment), sex (male vs. female) and stress (TSST vs. control condition) was conducted for negative mood. A significant main effect of stress ($F(1, 51) = 14.089$, $p < 0.001$) and a significant interaction between time and stress ($F(1, 51) = 11.006$, $p < 0.01$) occurred. The remaining effects did not reach significance (all $p > 0.05$). To investigate the significant interaction effect further *t*-tests were conducted. The TSST group reported more negative mood after the TSST ($t(55) = -4.257$, $p < 0.001$) but not before the TSST ($t(54) = -1.429$, $p = 0.159$) compared to the control group.

3.4. Ratings of the pictures

ANOVAs with the inner subject factors valence (positive vs. negative vs. neutral) and the between subject factors sex (male vs. female) and stress (TSST vs. control condition) were conducted for the ratings of arousal and valence of the pictures, conducted on

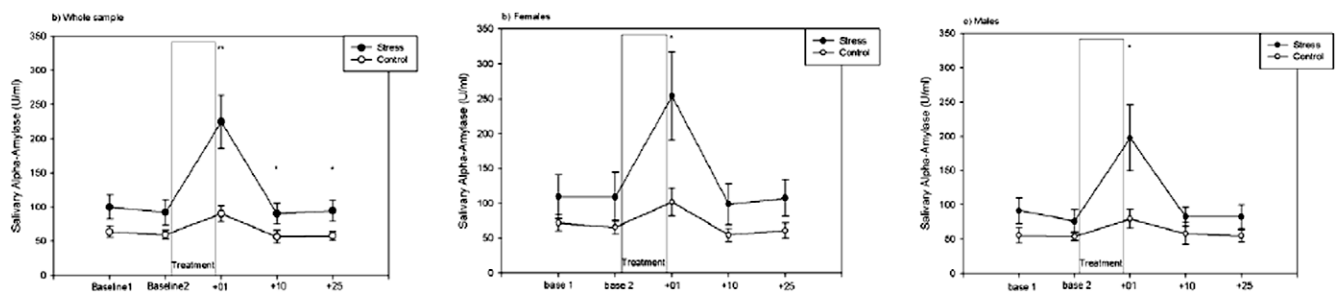


Fig. 3. sAA response (log transformed data) to the TSST and control condition. A significant interaction between stress and time occurred in the ANOVA. Follow-up *t*-tests showed significant differences between TSST and control group for (a) the whole sample, (b) females and (c) males at measurements +01, +10 and +25 (** $p < 0.001$; * $p < 0.05$).

day two. For valence a significant main effect of valence occurred ($F(2, 108) = 450.637, p < 0.001$). The remaining effects did not reach significance (all $p > 0.10$). Participants rated the positive items more positive than the neutral ($t(57) = 13.363, p < 0.001$) and negative ones ($t(57) = 24.078, p < 0.001$). Neutral items were rated as more positive than negative items ($t(57) = 23.621, p < 0.001$). For arousal a significant main effect of valence occurred ($F(2, 108) = 197.486, p < 0.001$). Again, the remaining effects did not reach significance (all $p > 0.10$). Participants rated the negative items as more arousing than the positive ($t(57) = 10.867, p < 0.001$) and neutral ones ($t(57) = 19.330, p < 0.001$). Positive items were rated as more arousing than the neutral ones ($t(57) = 9.314, p < 0.001$).

3.5. Effect of valence on immediate recall

To evaluate the influence of valence on initial acquisition an ANOVA with the factors valence (positive vs. negative vs. neutral), sex (male vs. female) and stress (TSST vs. control condition) was conducted for the immediate recall test, which occurred before the TSST or control condition. Results revealed a significant main effect of valence ($F(2, 108) = 39.313, p < 0.001$) and a significant main effect of sex ($F(1, 54) = 9.205, p < 0.01$). The remaining main and interaction effects did not reach significance (all $p > 0.05$). Paired *t*-tests showed that participants significantly recalled more negative than positive ($t(57) = 2.359, p < 0.05$) and neutral items ($t(57) = 8.067, p < 0.001$). Additionally more positive items were recalled than neutral items ($t(57) = 6.098, p < 0.001$). Women overall recalled more pictures than men ($t(56) = 3.086, p < 0.05$). Results are presented in Fig. 4.

3.6. Effects of post-learning stress on delayed free recall

For analyzes of delayed free recall we created a value which accounts for possible within and between subject variance in initial learning. Therefore free recall performance on the second day was expressed as the percentage of memory score in relation to the immediate recall score ((memory score on the second day/memory score on the first day) * 100; Kuhlmann et al., 2005; Kuhlmann & Wolf, 2005). Values above 100% thereby show an increase of memory over time (higher memory score on the second day), while values below 100% show decrease of memory (higher mem-

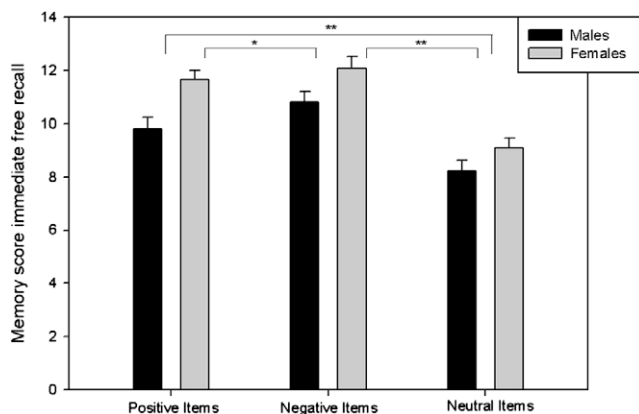


Fig. 4. Memory score for the immediate recall test for positive, negative and neutral items for the whole sample. An ANOVA revealed a significant main effect of valence and sex. Post-hoc *t*-tests showed that participants learned significantly more negative items than positive items (* $p < 0.05$) and neutral items (** $p < 0.001$). Positive items were better learned than neutral items (** $p < 0.001$). Overall women recalled more pictures than men ($p < 0.05$).

ory scores on the first day). This value was computed for positive, negative and neutral items separately.

To evaluate the influence of stress on memory an ANOVA was conducted with the factors valence (positive vs. negative vs. neutral), stress (TSST vs. control condition) and sex (male vs. female). A significant interaction effect between valence and stress occurred ($F(2, 108) = 3.910, p < 0.05$). No other significant effects could be observed (all $p > 0.10$). A post-hoc *t*-test was conducted to evaluate the significant interaction effect further. The TSST group showed better memory for the neutral items ($t(56) = 2.183, p < 0.05$) but not for the positive ($t(56) = 0.411, p = 0.682$) and negative ones ($t(56) = 1.135, p = 0.261$).

Additionally we conducted the ANOVA for each sex separately. A significant interaction effect between valence and stress was found in men ($F(2, 56) = 4.603, p < 0.05$) but not in women ($F(2, 52) = 0.585, p = 0.561$). The remaining effects did not reach significance (all $p > 0.10$).

Additional *t*-tests were conducted for the comparison between stress and control group for males and females separately. No significant difference occurred for positive (males: $t(28) = 0.462, p = 0.647$, females: $t(26) = 0.040, p = 0.969$) or negative items (males: $t(28) = 0.805, p = 0.427$; females: $t(26) = 0.813, p = 0.424$). However, for males a trend for a better recall of neutral items in the TSST group ($t(56) = 1.824, p = 0.079$) occurred. In females this effect was non-significant ($t(56) = 1.190, p = 0.245$).

The results for the entire sample as well as for women and men are separately presented in Fig. 5.

3.7. Effects of post-learning stress on delayed recall assessed with a multiple choice test

For the multiple choice test an ANOVA with the factors valence (positive vs. negative vs. neutral), sex (male vs. female) and stress (TSST vs. control condition) was conducted. Results revealed significant main effects of valence ($F(2, 108) = 17.472, p < 0.001$) and a significant interaction effect between sex and valence ($F(2, 108) = 8.509, p < 0.001$). No main effect of stress ($F(1, 54) = 1.702, p = 0.198$) and no interaction effects between stress and valence ($F(2, 108) = 1.539, p = 0.219$) were detected. The remaining effects did not reach significance (all $p > 0.10$) as well. Participants showed a better memory for negative than for positive ($t(57) = 4.838, p < 0.001$) and neutral items ($t(57) = 5.005, p < 0.001$). No differences emerged between positive and neutral items ($t(57) = 0.577, p = 0.566$).

Women remembered significantly more positive items than men ($t(56) = 4.158, p < 0.001$). No differences emerged for negative and neutral items (all $p > 0.10$).

3.8. Effects of post-learning stress on memory for gist and detail

To evaluate memory for gist and detail information an ANOVA with the inner subject factors valence (positive vs. negative vs. neutral) and gist (gist vs. detail) and the between subject factors sex (male vs. female) and stress (TSST vs. control condition) was conducted. Analysis revealed significant main effects of valence ($F(2, 108) = 19.250, p < 0.001$), gist ($F(1, 54) = 179.992, p < 0.001$) and a significant interaction effect between valence and gist ($F(2, 108) = 22.555, p < 0.001$). Additionally a significant main effect of sex was detected ($F(1, 54) = 5.958, p < 0.05$). No main effect and no interactions with stress could be observed (all $p > 0.10$). Results of *t*-tests revealed that overall women remembered more items than men ($t(56) = 2.454, p < 0.05$).

Results also revealed that more gist information was remembered for positive ($t(57) = 5.199, p < 0.001$), negative ($t(57) = 14.233, p < 0.001$) and neutral items ($t(57) = 4.959, p < 0.001$).

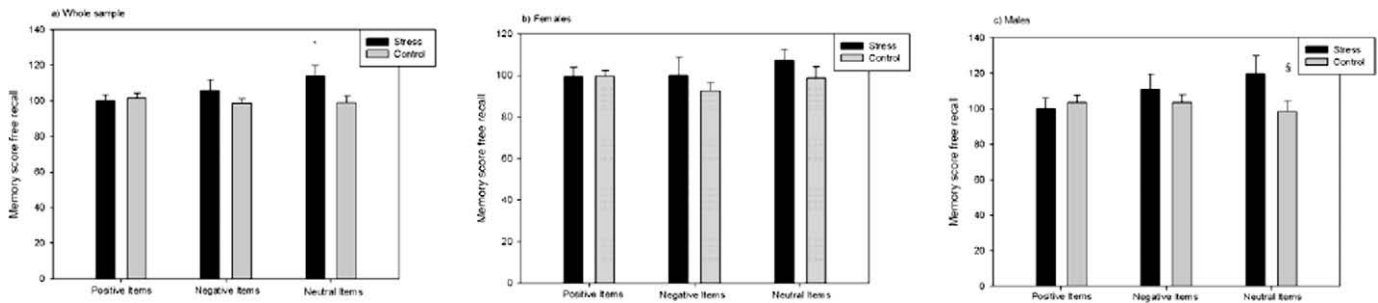


Fig. 5. Mean memory score for positive, negative and neutral items in the TSST and control group for (a) the whole sample, (b) females and (c) males. An ANOVA revealed a significant interaction between stress and valence in the whole sample and for the males. Follow-up *t*-tests showed a significant difference for the neutral items ($*p < 0.05$) in the whole sample and a trend for the males ($^{\S}p < 0.10$). Memory scores reflect the percentage of words recalled on the second day in relationship to the immediate recall assessed on the first day. Memory scores above 100% reflect an increase in memory, whereas memory scores below 100% reflect a decrease in memory.

3.9. Relationship between memory, mood, cortisol and alpha-amylase

To evaluate possible associations between the neuroendocrine and affective stress markers and delayed memory retrieval, bivariate Pearson's correlations were conducted. We computed a measure for the cortisol response (cortisol + 10 – cortisol baseline; Kirschbaum, Wolf, May, Wippich, Hellhammer, 1996; Wolf et al., 2001). Higher values indicate a stronger response to the TSST. Similarly, we also created a value for the response between baseline and the highest value (sAA + 01 – sAA baseline) for alpha-amylase. Additionally a measure for negative mood increase (negative mood after TSST – negative mood before TSST) was computed. Again higher values indicate a stronger increase of negative mood. For the second day a mean value was conducted for the two cortisol samples ((pre + post)/2). This was done to create a single measure indicative of the basal cortisol level on the day of retrieval testing.

The cortisol response was significantly correlated with memory for neutral items. This was the case for the entire group as well as for males and females separately. For negative items a trend ($0.10 < p < 0.05$) emerged for the analysis including the entire group, while no association was observed when the two sexes were analyzed separately. Results are presented in Table 1. Cortisol levels during retrieval (day 2) were not significantly ($p > 0.10$) associated with any of the memory measures (data not shown).

In order to ascertain that the observed correlations are not simply reflective of the group differences between the stressed group and the control group, partial correlations were conducted controlling for the grouping factor stress (TSST vs. control). For the entire sample, the correlation between the cortisol response and memory for neutral items was still significant ($r = 0.406$, $p > 0.01$). The correlations between cortisol and memory for positive ($r = 0.093$, $p = 0.491$) and negative ($r = 0.210$, $p = 0.118$) items were non-significant. When the sample was split according to sex the relationship between cortisol and memory for neutral items was still significant in men ($r = 0.391$, $p < 0.05$) but turned into a non-significant trend in women ($r = 0.343$, $p = 0.08$). The correlations be-

tween cortisol and memory for positive (males: $r = 0.044$, $p = 0.822$; females: $r = 0.205$, $p = 0.306$) and negative (males: $r = 0.216$, $p = 0.260$; females: $r = 0.081$, $p = 0.687$) items also remained non-significant.

No significant correlations were detected between mood and memory performance or sAA and memory performance (all $p > 0.10$).

4. Discussion

The aim of the present study was to assess the influence of post-learning psychosocial stress on memory consolidation of positive, negative and neutral pictures. Additionally, possible sex differences were evaluated. Results demonstrate that psychosocial stress elicited a significant neuroendocrine stress response in men and women. In both sexes cortisol and alpha-amylase levels were elevated after the TSST. However, the cortisol stress response was more pronounced in men. Additionally, an affective reaction to the TSST was observed with both sexes reporting more negative mood after the TSST. With respect to memory post-learning, stress enhanced the consolidation of neutral items but did not significantly affect memory for positive or negative items. This interaction effect was significant in the whole sample as well as in the male group. In support of these group comparisons, correlations were found between the cortisol stress response and memory for neutral items in the free recall test for the entire sample, as well as for both sexes separately. Additionally, a trend for a correlation between cortisol response and memory for negative items occurred for the whole sample. No effect of stress was found for the multiple choice test or the separate analysis of memory for gist and details assessed with the multiple choice test.

The finding of a neuroendocrine response to the TSST is well in line with the literature reporting an enhanced release of cortisol and salivary alpha-amylase in response to psychosocial stress (Dickerson & Kemeny, 2004; Kudielka, Schommer, Hellhammer, & Kirschbaum, 2004; Nater et al., 2006; Rohleder et al., 2004). In

Table 1

Correlation coefficients and *p*-values for the correlations between memory scores in the delayed free recall test and cortisol response on day 1 (learning session).

		Positive items delayed free recall	Negative items delayed free recall	Neutral items delayed free recall
Cortisol response (day 1)	Whole sample	$r = 0.042$	$r = 0.256$	$r = 0.480$
	$n = 58$	$p = 0.755$	$p = 0.053$	$p < 0.001^{**}$
	Males	$r = -0.030$	$r = 0.258$	$r = 0.492$
	$n = 30$	$p = 0.874$	$p = 0.169$	$p < 0.05^{\circ}$
	Females	$r = 0.173$	$r = 0.149$	$r = 0.403$
	$n = 28$	$p = 0.379$	$p = 0.450$	$p < 0.05^{\circ}$

$^{\circ} p < 0.05$.

$^{**} p < 0.001$.

addition to the physical response to the stressor, an increase of negative mood was observed which indicates an emotional arousal in response to the TSST (Abercrombie, Speck, & Monticelli, 2006). In the present experiment women showed a weaker cortisol response to the TSST than men. This is in agreement with several studies that demonstrate a weaker salivary cortisol response to performance based stressors in women than in men (Kirschbaum, Pirke, & Hellhammer, 1995; Kirschbaum et al., 1996; Kirschbaum et al., 1992; Stroud et al., 2002, but see Kelly et al., 2008). No sex differences were detected for salivary alpha-amylase, which is in contrast to a recent report of overall higher sAA levels in men (van Stegeren et al., 2008). In sum, the present results demonstrate that the TSST induced a robust neuroendocrine and affective stress response. For cortisol, but not for the other two stress markers (sAA and mood), the response was more pronounced in men.

The present study reports an enhanced memory consolidation after psychosocial stress treatment. Post-encoding stress is known to enhance memory consolidation in rodents (Akirav et al., 2001; Akirav et al., 2004; Roozendaal et al., 1999; Roozendaal et al., 2001; Sandi et al., 1997) and humans (Andreano & Cahill, 2006; Beckner et al., 2006; Cahill et al., 2003; Smeets et al., 2008). However, in the present study, this beneficial effect was restricted to neutral items and no significant effect was found for positive or negative items. This result was somewhat unexpected, as the beneficial effects of cortisol have often been found to be more pronounced for emotional items. An enhanced memory for emotional items was observed after cortisol treatment (Buchanan & Lovallo, 2001; Kuhlmann & Wolf, 2006b) or post-learning stress (Abercrombie et al., 2006; Cahill et al., 2003; Smeets et al., 2008). It has therefore been assumed that arousal caused by the learning material potentiates the effects of stress and elevated GCs on memory (Roozendaal et al., 2006). However, in our study the opposite picture emerged. We found stress effects on the non-arousing neutral items, but no significant effect on the arousing positive and negative ones, even though a numeric trend could be observed for negative items. Moreover, the correlational analysis revealed a trend between the stress induced cortisol rise and memory in the free recall test for negative items. This association would be in line with previous reports on a post-learning stress induced consolidation enhancement for negative items (Cahill et al., 2003; Smeets et al., 2008). It suggests that the failure to find an effect on negative items at the between group level might be caused by specifics of the used task, which might not have been sensitive in detecting the beneficial effects on the negative items.

Several studies observed an enhanced memory for both kinds of stimuli after pre-learning cortisol treatment (Abercrombie, Kalin, Thurow, Rosenkranz, & Davidson, 2003) or for neutral stimuli after post-learning stress, when only neutral stimuli were presented (Andreano & Cahill, 2006; Beckner et al., 2006). The present finding of an effect on the neutral stimuli therefore, is in line with these studies but the unanswered question is why we did not detect an effect on emotional items.

One explanation could be differences in acquisition. At the time of immediate recall we found, as expected, an emotional enhancement effect. Positive and negative pictures were significantly better remembered than neutral ones. This emotional enhancement effect did not further increase between the immediate and delayed recall, which is in contrast to some previous studies (e.g. Quevedo et al., 2003), but in line with previous studies from our group (Kuhlmann & Wolf, 2006b). The stress group recalled more neutral items in the delayed recall test, compared to the immediate recall test. Thus, in this task, post-learning stress not only prevented forgetting but actually boosted memory consolidation leading to a superior memory performance 24 h after the original presentation of the slides. One interpretation of our findings could be that stress especially enhances weak or fragile memory traces. Having said

this it must be acknowledged that due to their better initial encoding, emotional memories had less room for a further improvement due to post-learning stress (possible ceiling effect).

In the present study we used pictures which were accompanied by a narrative. Here, the stimuli formed a complex episode and are somewhat comparable to the stimuli used by Andreano and Cahill (2006) who also found an effect of stress on neutral material. The specific effects of post-learning stress or pre-learning cortisol treatment on emotional memory were obtained in studies using a larger number of slides, which were presented without the additional presentation of verbal information (Cahill et al., 2003; Kuhlmann & Wolf, 2006b). This rather long presentation interval might lead to a deeper processing. The absence of forgetting during the 24 h delay strengthens the assumption of a deep encoding. In most studies participants perform better in the immediate recall test compared to the delayed recall test (Kuhlmann & Wolf, 2005; Kuhlmann et al., 2005). In the present study, no forgetting took place which might be due to deep encoding and the relatively small number of slides used. Our overall findings are somewhat similar to a recent study from Buchanan and Tranel (2008), where the authors used a slightly modified version of this task containing 20 pictures (ten neutral and ten negative). Similar to our findings the authors of this study observed little to no forgetting over a 24 h delay. In addition pre-retrieval stress had an impact on memory, which however was not specific to the emotionally arousing pictures.

A different explanation might be that the observed effects are due to an inverted U-shape relationship between cortisol and arousal (Baldi & Bucherelli, 2005). Arousal is associated with noradrenergic activation in the basolateral amygdala and this activation is thought to be a prerequisite for the effects of GCs on memory (de Quervain, Aerni, & Roozendaal, 2007; Kuhlmann & Wolf, 2006a; Roozendaal et al., 2006). A recent study of ours using the identical learning material observed that basal cortisol levels were positively associated with memory for arousing pictures but not for neutral ones (Preuss et al., in press). In this study no stressor was used and therefore effects rely on the arousal, which is induced by the learning material. Our present finding could suggest that cortisol can exert its positive effects on memory consolidation only at an optimal arousal level. This optimal level might reflect the interaction of arousal induced by the learning material with arousal induced by the experimental manipulation. In situations where there is no stressor, cortisol enhances memory for items that induce arousal but not for items which lack this arousal (Buchanan & Lovallo, 2001; Kuhlmann & Wolf, 2006b; Preuss et al., in press). In situations with a mild stressor (e.g. cold pressure stressor) this scenario might still take place. However in the case of a strong psychological stressor (e.g. the TSST) neutral items might have the optimal arousal level, while the arousing positive and negative items are shifted to the right side of the inverted U-shape. Anticipation of and, even more, participating in a strong stressor might therefore cause the effects observed on neutral items in the present study. Probably cortisol affects consolidation of non-arousing neutral items only under circumstances of strong external induced arousal. The assumption of an inverted U-shape function for arousal might explain some of the inconsistent results in the field of cortisol and arousal but this hypothesis needs further evaluation and is not consistent with all previously published findings.

Effects of post-learning stress were restricted to the free recall test. No influence of stress or GCs on memory performance in the multiple choice test was detected. The finding of an unaffected performance in cued recall tests is in line with several previous stress or cortisol studies (e.g. de Quervain et al., 2003; Kuhlmann & Wolf, 2006b; Kuhlmann et al., 2005). Evidence has been provided that recollection and recognition are mediated by different brain structures (hippocampus vs. perirhinal cortex; Aggleton & Brown,

2006). Knowing that the hippocampus is especially sensitive to the effects of stress, it is not surprising to find the strongest effects for free recall.

Additionally, in the cued recall test, we observed no effect on gist or detail aspects of this task. This is in contrast to previous pre-learning stress studies which reported that stress impaired memory for the gist but not for details of a story or even increased the number of details remembered (Cahill et al., 2003; Payne et al., 2006). This might suggest that the task used to differentiate between gist and details in the present study was not sensitive to stress effects. Thus more research is needed in order to understand whether or not stress differentially affects information for details.

An additional aim of the present study was to evaluate possible sex differences in the effects of stress on memory consolidation. Results indicate slight differences between men and women. While the overall ANOVA did not reveal a significant sex by treatment interaction, separate analyzes for men and women indicated a significant effect of stress on memory for men but not for women. For men we found a beneficial effect of stress on memory for neutral items. In women the effects were smaller and non-significant. It has been demonstrated in several studies that sex differences exist for the influence of stress on memory or emotional learning. The effects of stress were often more pronounced for men than for women (Andreano & Cahill, 2006; Cahill, 2003; Jackson et al., 2006; Stark et al., 2006; Wolf et al., 2001; Zorawski et al., 2006). In our study, the smaller cortisol response to the stressor is the most likely mechanism behind the observed sex differences, since the effects in women were descriptively rather similar to the results obtained in men. In support of this conclusion we observed, in both sexes, an association between the cortisol response and memory consolidation for neutral pictures.

Due to pragmatic reasons women were tested at every phase of the menstrual cycle in our current study with the exception of menses. A recent report suggests that only during the luteal phase correlations between cortisol and memory might be detectable (Andreano, Arjomandi, & Cahill, 2008). However, the literature on this topic is heterogeneous and opposing results (no associations in the luteal phase) have been reported as well (Wolf et al., 2001). Moreover Smeets et al. (2008) as well as Preuss et al. (in press) reported an association between cortisol and memory consolidation in a sample of women not further characterized with respect to their hormonal status. Finally, in the present study, the cortisol stress response was associated with memory consolidation in women, even though not as strong as it was in men. In sum, even though the empirical situation on the impact of the menstrual cycle on stress induced memory changes is far from clear, menstrual cycle associated alterations might have contributed to the smaller effects of the stressor on memory consolidation in the women group.

There are some limitations of the current study. First, our sample size of 28 women and 30 men is certainly not large enough to exclude the possibility that non-significant findings might be secondary to a lack of power. Second, as mentioned above, we did not control for menstrual cycle stage (except of menses), which might have increased the variance in our group of women. In order to evaluate the influence of menstrual cycle associated changes in gonadal steroids on the observed effects, sex hormones should be measured in future studies on this topic whenever possible (Andreano et al., 2008). Third, more objective psychophysiological measures (e.g. skin conductance) of arousal could be helpful in clarifying the obviously quite complex association between stress and the emotional arousal of the learning material (Cahill et al., 2003). Fourth, the number of items presented (five per valence category), together with the choice of a delay of 24 h between immediate and delayed recall might have resulted in a task which was almost too easy for the subjects. This problem is illustrated in

the failure to find forgetting during the delay period. Especially for emotionally arousing items there might not have been enough room in order to detect a stress induced consolidation enhancement as observed in previous studies (Cahill et al., 2003; Smeets et al., 2008). Future studies on this topic should use memory tasks with more items and/or a longer retention interval.

In sum, the current study reports on the beneficial effect of post-learning stress on the consolidation of neutral stimuli. In contrast, positive and negative stimuli were not affected. Thus, our study illustrates that the effects of stress on memory are not always stronger for emotional material. We have discussed several methodological and theoretical explanations for the specificity of the effects for neutral material observed in this study. Additional experiments are needed to disentangle the factors determining the consolidation of memories acquired directly prior to stress.

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