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Effects of acute psychosocial stress on the neural correlates of episodic encoding: Item versus associative memory

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ABSTRACT

Acute stress is known to modulate episodic memory, but little is known about the extent to, and the circumstances under, which stress affects encoding of item vs. inter-item associative information for words of different valences. Furthermore, the precise neuro-cognitive mechanisms underlying stress effects on episodic encoding in humans are largely unknown. To address these questions, in the present study we recorded EEG activity while male participants encoded neutral, negative and positive words, each paired with another word that was always neutral. Immediately before encoding, half of the participants experienced a psychosocial stressor, the Trier Social Stress Test, while the other half underwent a control procedure. Twenty-four hours later, participants completed separate item and associative recognition tests. Pre-learning stress enhanced item recognition accuracy for the positive, but not for the negative words. By contrast, there was no evidence for stress effects on associative recognition. The increase in item recognition was accompanied by a higher familiarity-, but not recollection-, based item retrieval of positive and neutral, but not negative words. Crucially, in the event-related potential (ERP) stress affected the amplitude of the frontal slow wave in general, and the frontal slow wave subsequent memory effect for positive words in specific, and the subsequent memory effect was correlated with cortisol levels after the stress manipulation. Our results suggest that positive words are encoded more elaboratively under stress, leading to a higher likelihood of subsequent item retrieval. An interaction of cortisol with frontal-lobe dependent control processes as well as a shift in attentional biases may contribute to this stress-induced modulation of episodic encoding.

1. Introduction

Acute stress temporarily changes how we perceive, learn and retain new information. One cognitive function that is particularly sensitive to stress is episodic memory. Thus, a stressor that occurs immediately before learning typically enhances the probability of successfully retrieving the learned material in an episodic memory test after a delay (e.g., Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012, for a review). The effect of pre-learning stress on memory is dependent on factors like the delay between the stressor and encoding (Shields, Sazma, McCullough, & Yonelinas, 2017), resulting in the question to what extent pre-learning stress differentially affects encoding vs. subsequent consolidation of studied information. The goals of the present study are, first, to gain a better understanding of the circumstances under which stress affects episodic encoding, and second, to identify neuro-cognitive mechanisms that are affected by stress, leading to modulations of memory encoding.

Physiologically, stress activates the hypothalamic-pituitaryadrenal-axis (HPA-axis) on the one hand, leading to the secretion of glucocorticoids (cortisol), and the sympathetic nervous system on the other hand, resulting in a release of norepinephrine (NE). One model postulates that modifications of memory due to stress experienced before learning are caused by a boost in consolidation due to an interaction of cortisol and NE in the human amygdala, which in turn interacts with other brain regions (Roozendaal, Okuda, De Quervain, & McGaugh, 2006). When a stressor is relatively brief, there is, however, only a short time window during which the levels of both neuroendocrines are elevated: NE is secreted quickly and returns to baseline soon afterwards, while cortisol levels rise slowly and remain elevated for a longer duration (e.g., Kirschbaum, Pirke, & Hellhammer, 1993). Emotional stimuli lead to secretion of NE (Berridge & Waterhouse, 2003) even if they are encountered in the absence of stress. If this stimulus-induced NE release co-occurs with stress-induced cortisol, a boost of subsequent memory performance can occur even after the rise in NE due to the

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stressor has returned to baseline (Roozendaal et al., 2006). This model can therefore account for the commonly reported pattern that only emotional material benefits from pre-learning stress (e.g., Cornelisse, van Stegeren, & Joëls, 2011; Merz, 2017; Schwabe, Böhringer, Chatterjee, & Schächinger, 2008; Zoladz et al., 2011).

1.1. Effects of pre-learning stress on memory: dependence on valence

NE secretion in response to arousing, motivationally significant stimuli is observed regardless of their affective valence (Berridge & Waterhouse, 2003), so according to the consolidation model, pre-learning stress should be observed for positive and negative stimuli alike. In contrast to this prediction, some previous studies have reported pre-learning stress effects selectively either only for positive (e.g., Zoladz et al., 2011) or only for negative (e.g., Merz, 2017) stimuli, but not for both. Other studies have shown an enhancing effect of post-learning stress for neutral rather than emotional material (Schwabe et al., 2008; Yonelinas, Parks, Koen, Jorgenson, & Mendoza, 2011). In general, prior results therefore seem to suggest that effects of pre-encoding stress are valence-specific, but are inconsistent in the precise pattern. Additional systematic research on this issue should dramatically enhance our understanding of the mechanisms of stress-learning interactions.

1.2. Effects of pre-learning stress on item vs. associative memory

Notably, stress experienced around the time of learning has in some studies affected performance in simple recognition tests, but not in free recall tests (McCullough & Yonelinas, 2013; Merz, 2017; Yonelinas et al., 2011; Zoladz et al., 2011). Although in a meta-analysis, pre-encoding stress effects on memory were not significantly moderated by test format (Shields et al., 2007), few studies have systematically explored a potential difference. We propose that to understand the potential differential stress effects on learning better, it is useful to consider the distinction between episodic memory for item information and for associations between items (inter-item associations). These two types of episodic memory have been dissociated in behavioral (Yonelinas, 1997), neuroimaging (Davachi & Wagner, 2002), event-related potential (ERP; Kamp, Bader, & Mecklinger, 2017), and patient studies (Bowles et al., 2007; Vargha-Khadem et al., 1997), and show different developmental trajectories across the lifespan (e.g., Old & Naveh-Benjamin, 2008). Importantly, free recall heavily depends on inter-item associations (Kahana, 1996; Raaijmakers & Shiffrin, 1981), while standard recognition tasks rely more strongly on item memory (Gillund & Shiffrin, 1984). A boost of pre-learning stress on recognition, but a weaker effect on recall, could therefore be due to a selective benefit of item, but not associative, memory.

A similar idea, that item- but not associative memory benefits from the presence of (negative) emotion, has been put forward by Bisby, Horner, Hørlyck, and Burgess (2016), and in the present study we examined whether this idea extends to the effect of acute pre-learning stress on memory. Taking into account the dependence of associative memory on the hippocampus (e.g., Davachi, 2006), the idea is consistent with a shift away from hippocampus-based learning modes under stress (Kim & Diamond, 2002; Schwabe & Wolf, 2011), although this finding has not been extended to episodic memory. Furthermore, information that is learned in close proximity to an acute stressor is often more likely to be retrieved based on familiarity (rather than recollection; McCullough & Yonelinas, 2013; Yonelinas et al., 2011; but see Wiemers, Sauvage, Schoofs, Hamacher-Dang, & Wolf, 2013). Since familiarity and recollection can both support item memory, while associations must typically be retrieved by means of recollection (Yonelinas, 1997), this also supports the idea that item- but not associative memory benefits from pre-learning stress.

Previous attempts to directly dissociate the effects of pre-learning stress on item vs. associative memory are rare. As one exception, Guez, Saar-Ashkenazy, Keha, and Tiferet-Dweck (2016) tested item vs. associative memory in separate recognition tests in a learning task that followed a stressor (vs. a control condition). Unfortunately, repeated study-test cycles followed the stress induction, so that both encoding and retrieval phases occurred while the physiological stress response was elevated. This complicates the interpretation of the results, because stress typically hinders retrieval (for a review, see Schwabe et al., 2012). An even more recent study, which did not suffer from this limitation, also tested the effects of acute stress before and after learning, and before retrieval, on item and associative memory for pairs of negative words with neutral images (Goldfarb, Tompary, Phelps & Davachi, in press). They found that pre-encoding stress enhanced associative memory for word-object pairs that were subjectively perceived as highly arousing, but did not affect item memory for the negative words. However, in this study, valence was not manipulated. Furthermore, in the design of this study, the pre-learning and post-learning stress conditions were realized in a single session, and it is unclear how this may have affected the results. More research is clearly needed to examine this question. Finally, the additional examination of ERP activity in our study should lead to invaluable novel mechanistic insights (see Section 1.4).

1.3. Effects of pre-learning stress on familiarity and recollection based retrieval

In order to understand stress effects on encoding better, it is also useful to examine the manner in which the encoded information is subsequently retrieved on the basis of dual-process models of memory retrieval. To this end, in the present study we calculated Receiver-Operating Characteristics (ROCs) for an item and an associative recognition test, and estimated parameters of recollection- and familiarity-based retrieval (for a review, see Yonelinas & Parks, 2007). Few prior studies have examined stress-effects on memory using ROC-based estimates of recollection and familiarity (McCullough & Yonelinas, 2013; Wiemers, Hamacher-Dang, Yonelinas, & Wolf, 2018; Wiemers et al., 2013), and none of them specifically looked at pre-learning stress effects on subsequent recollection- vs. familiarity-based retrieval in item vs. associative memory tests. We hypothesized that pre-learning stress selectively enhances familiarity-based retrieval of emotional stimuli in an item recognition test. Recollection, on the other hand, should be either reduced or unaffected by pre-learning stress.

1.4. ERPs as neuro-cognitive correlates of episodic encoding

Changes in encoding due to stress should be rooted in modulations of neuro-cognitive processes during learning. Specifically, stress-induced changes in ERPs can occur even without detectable changes in behavior (e.g., Paul et al., 2018; Weymar, Schwabe, Löw, & Hamm, 2012), suggesting that they are a more sensitive measure than behavior. Another advantage of recording ERP activity during encoding is that, unlike performance in a later memory test, they provide a real-time measure of neural processes at encoding that are not influenced by subsequent consolidation. Finally, an examination of the effects of stress on ERP components whose functional significance has been well-characterized in prior research allows for insights into the cognitive (sub-)processes that are altered by stress, thereby providing a deeper understanding of *why* and *how* stress affects episodic encoding.

If an ERP component is relevant to episodic encoding, it should be larger in amplitude for stimuli that are subsequently successfully retrieved than for stimuli that are not ("subsequent memory effects", SMEs; e.g. Karis, Fabiani, & Donchin, 1984; Paller & Wagner, 2002). A component often observed to show an SME is a frontally distributed negative-going slow wave, which appears to reflect higher-order control processes (Bosch, Mecklinger, & Friederici, 2001). Thus, a frontal slow wave SME is particularly pronounced when words are encoded by means of semantic and/or associative elaboration, as opposed to

simpler learning strategies (e.g., Fabiani, Karis, & Donchin, 1990). Kamp et al. (2017) proposed that the frontal slow wave SME reflects processes involved in different kinds of elaborative processing, including the formation of associations of study items with previous knowledge. If pre-learning stress leads to a more elaborate memory trace, this should be reflected in an enhanced frontal slow wave SME.

1.5. The present study

After a psychosocial stressor or a control procedure, participants completed an incidental encoding task on word pairs containing a neutral, a negative or a positive word in the second position, while their EEG was recorded. Twenty-four hours later, participants completed separate item and associative recognition tests. We hypothesized that pre-encoding stress would enhance item, but not associative, memory, and that this effect would be exclusive to emotional words. Due to the inconsistency of prior results, we did not make any directed predictions about the effects of valence. Furthermore, we hypothesized that stress would enhance frontal slow wave amplitudes and SMEs.

2. Method

All procedures were in line with the Declaration of Helsinki and followed ethical standards of the German Psychological Association. The local ethics committee at Saarland University, where all experimental procedures were carried out, approved the study.

2.1. Participants

Since there are well-known sex differences in stress reactivity (for a review, see Liu et al., 2017), in the present study we recruited only male participants. Twenty-eight participants took part in a pre-study rating task (age: $M = 24.21$). A different set of 37 males participated in the main experiment, of which 19 were assigned to the stress group and 18 to the control group. The participants in the main experiment were between 19 and 30 years old (control group: $M = 23.67$, $SD = 3.24$; stress group: $M = 23.35$, $SD = 2.95$), had normal or corrected-to-normal vision and did not have any history of neurological disorder or injury. They were instructed not to eat anything or drink any coffee for 2 h before the start of their session, and to abstain from drinking alcohol the day before. Participants in the main experiment were paid 8 Euro per hour or received partial course credit for their participation.

2.2. Procedure

All sessions took place between 12 and 6 pm, because stress reactivity is higher in the afternoon than in the morning (e.g., Dickerson & Kemeny, 2004). Upon arrival in the laboratory, participants signed an informed consent form, which among other information about the study informed them which of the two groups they were assigned to. The subsequent preparations for the EEG recording took up to 45 min. This was followed by either the Trier Social Stress Test (TSST; Kirschbaum et al., 1993) or a control condition with similar task characteristics, which does not activate the HPA-axis (modeled after the "friendly" TSST; fTSST; Wiemers, Schoofs, & Wolf, 2013). During the TSST or fTSST, the EEG cap was disconnected from the amplifier and the participant stood upright.

For the TSST, the experimenter informed the participant that they would have to give a job interview in front of two judges (of which one was the experimenter herself), while being videotaped for a subsequent analysis. After three minutes of preparation, during which the participant was alone in the laboratory, an unfamiliar female judge and the experimenter, both wearing white lab coats, entered the room and took a seat at a table across from the participant. The experimenter explained the procedure, adjusted the microphone and started the video recording (note that in reality no video was recorded). Then, the participant began their free interview speech, which lasted 5 min. Afterwards, participants counted aloud backwards in steps of 17 starting at 2023 for another 5 min. The unfamiliar judge took the role of the interview leader, and her behavior followed typical procedures (Kirschbaum et al., 1993).

Participants in the control group completed a modified version of the fTSST. Instead of a job interview, participants talked about their last vacation for 5 min in front of a single female confederate who acted friendly and responsive, and wore colorful clothes. Afterwards they solved an easy arithmetic task for 5 min.

Upon completion of the TSST/fTSST, the judges left the room and the participant took a seat in front of a computer in an electrically shielded, sound attenuated chamber within the same lab room. The EEG cap was re-connected with the amplifier, and the participants completed an incidental encoding task, which took about 30 min. Afterwards, the EEG cap was removed and the session ended.

Twenty-four hours later the participants returned to the laboratory and completed a surprise recognition phase consisting of an item test and an association test. No EEG was recorded. The second session lasted up to one hour.

2.3. Stimuli

Stimuli were drawn from the database by Lahl, Göritz, Pietrowsky, and Rosenberg (2009), which includes valence and arousal norms for individual German words, and consisted of noun pairs of which the first word was emotionally neutral and the second word was either neutral, positive or negative. Neutral words presented in the first position of a pair (n = 270) were of low arousal ($M = 2.16$, $SD = 0.58$) and of medium valence ($M = 5.08$; $SD = 0.28$). Neutral words shown in the second position of a pair (n = 90) exhibited similar characteristics (arousal: $M = 2.14$, $SD = 0.58$, valence: $M = 5.01$, $SD = 0.33$). Positive words (n = 90) were of high arousal ($M = 6.19$, $SD = 0.76$) and high valence ($M = 7.61$, $SD = 0.64$) and negative words (n = 90) were of high arousal ($M = 6.34$, $SD = 0.86$) and low valence ($M = 2.37$, $SD = 0.64$). All words were 4–9 letters long and the groups of positive, negative and neutral words presented in the second position of a pair were matched for concreteness, length and frequency. Positive and negative words did not differ in arousal.

We obtained pre-experimental ratings to insure that the two words of each pair were pre-experimentally unrelated. Each pair was rated for semantic relatedness on a scale of 1 ("strongly related") to 4 ("very unrelated") by at least 7 participants. Word pairs were accepted as unrelated if at least 70 percent of the participants rated them as either "very unrelated" or "unrelated". The remaining pairs were re-arranged and again rated by a different set of participants. Altogether, this resulted in 270 unrelated word pairs (90 neutral-neutral; 90 neutral-positive and 90 neutral-negative).

2.4. Encoding and recognition tasks

The incidental encoding task was designed to stimulate encoding of both item and associative information. Participants were asked to silently generate a sentence with each of 180 word pairs (60 neutral-neutral; 60 neutral-positive and 60 neutral-negative) presented in random order and rate for each pair how well they were able to generate a sentence on a scale of 1 ("very well") to 4 ("very poorly"; the rating scale was reversed for half of the participants). Each trial (Fig. 1A) began with the presentation of a fixation cross in the center of the screen for 2000 ms, replaced by the first word of the pair for 400 ms. Next, a fixation cross was shown for 1500 ms, followed by the second word of the pair for 400 ms. After another fixation cross shown for 1500 ms the rating screen was displayed. Participants provided their rating using four keys on a standard computer keyboard, thereby terminating the rating screen, and the next trial began. There were four blocks containing 45 word pairs each in the encoding task, which were

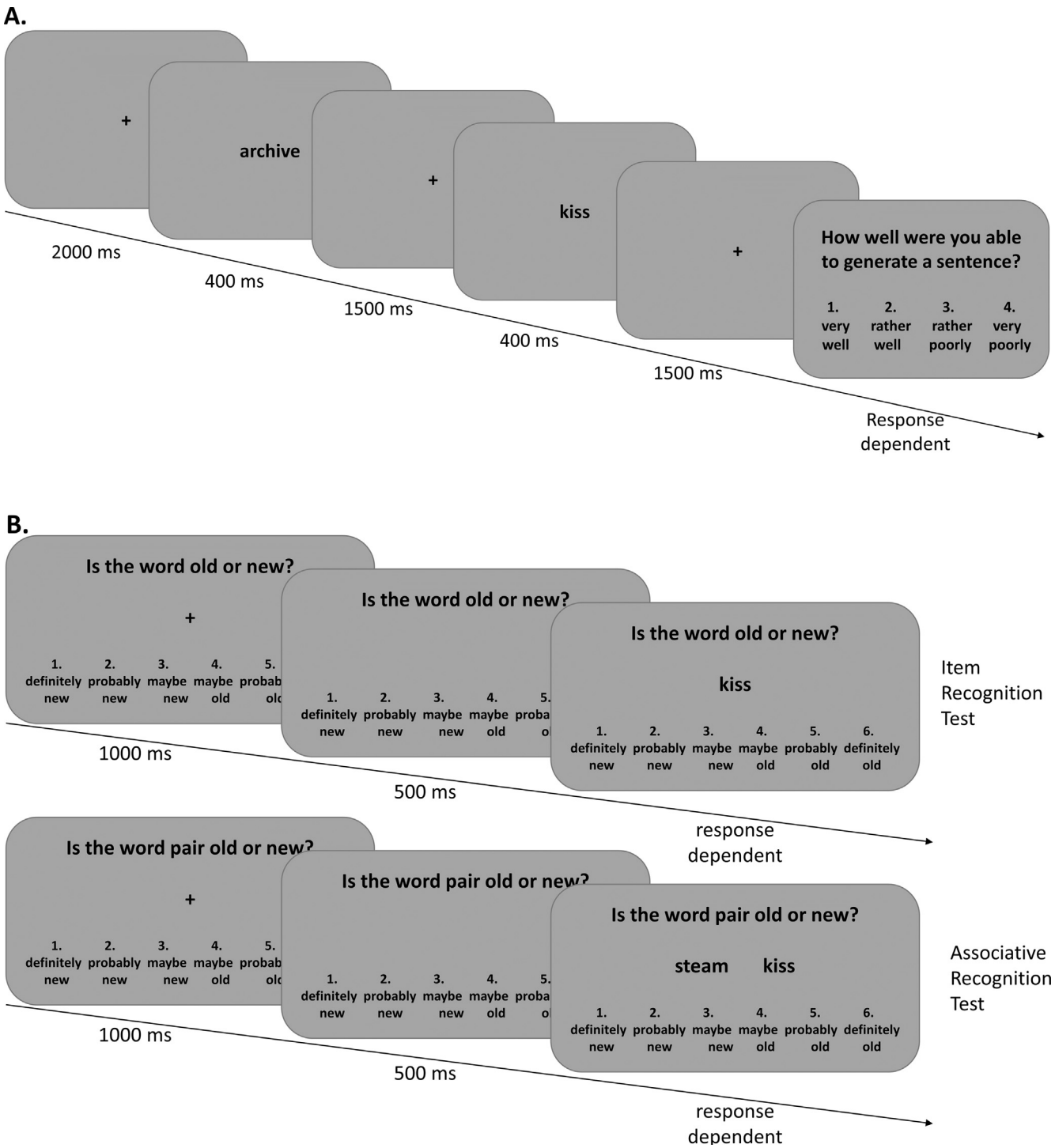

Fig. 1. Study design. A. Sequence of a single trial in the study phase. Neutral-positive, neutral-negative and neutral-neutral pairs (a total of 180 pairs) were shown in random order. The Figure shows a neutral-positive word pair. B. Sequence of a trial in the item recognition test and of a trial in the associative recognition test. In the item recognition test, previously studied (old) items were shown among non-studied (new) items. Only items from the second position of the study pairs were tested. The correct response in the displayed trial is "old" (4–6). In the associative recognition test, previously studied (old) pairs were shown among re-combinations of two old words into a new pair. The correct response in the displayed trial would be "new" (meaning that the pairing of the two words in the pair is not as the pair was studied). Note that the stimuli have been translated from German to English.

separated by self-paced breaks.

On the second day, participants completed two recognition tests (Fig. 1B). In the item test, all 180 words that were presented in the second position of a pair during encoding were presented in a random sequence together with 90 unstudied words (30 neutral, 30 negative and 30 positive) drawn from the same item pool as the previously studied words. A trial consisted of a fixation cross for 1000 ms, followed by a blank screen for 500 ms, and then the probe word, all presented in the center of the screen. Above the center of the screen, the question "Is this word old or new?" was continually shown, and below the word, the rating scale was displayed, ranging from 1 ("definitely new") to 2 ("probably new") to 3 ("maybe new") to 4 ("maybe old") to 5 ("probably old") to 6 ("definitely old"; the scale was reversed for half of the participants). The participant provided the response on a standard

computer keyboard and the response terminated the screen. Breaks were allowed after each set of 45 trials.

The associative recognition test was always completed after the item recognition test and consisted of 120 pairs (40 neutral-neutral, 40 neutral-positive, 40 neutral-negative) that had been studied in this exact pairing on day 1. Furthermore, 20 pairs of each category were recombined such that, for example, a neutral word presented previously with a negative word was recombined with a negative word from a different study pair. Note that this procedure was identical between the two groups, and that the second word of each pair had already been tested in the item test. Therefore, the fact that the item test preceded the association test should not affect any main effect of stress or emotionality. Presentation order of the pairs in the association test was random. A trial consisted of a fixation cross (1000 ms), followed by a blank screen (500 ms) and finally the two words of a pair presented simultaneously to the left and right of the center of the screen. Above the pair, the question "Is the word pair old or new?" was shown continually, and below the pair the same rating screen as for the item recognition test was shown. Participants were instructed to judge a pair as "old" only if it had been presented in this exact pairing during the study phase, but to provide a "new" judgment if it consisted of a recombination of previously studied pairs. The response terminated the screen and the next trial began. Breaks were allowed after each set of 30 trials.

The 270 word pairs were presented in a counterbalanced manner during encoding (180 pairs) and as foils in the item recognition test (only the second item of a pair, 90 words total). Therefore, words presented during encoding for some participants were presented as recognition foils for other participants and vice versa. During all tasks, stimuli were presented in black Arial font, size 32, on a grey background.

2.5. Measures of the stress response

To capture the stress response, we took saliva samples at 6 time points for subsequent cortisol analyses. These time points were (1) after signing the informed consent form (−40 min respective to the onset of the TSST/fTSST), (2) immediately before the TSST/fTSST (0 min), (3) immediately after completion of the TSST/fTSST (+15 min), (4) during the second break of the encoding task (+30 min), (5) after the encoding task (+45 min) and (6) upon arrival in the laboratory on day 2. In addition, participants completed the "positive and negative affective schedule" (PANAS; Krohne, Egloff, Kohlmann, & Tausch, 1996) at time points 1, 3, 5 and 6, which we separately analyzed for the positive affect (PA) and negative affect (NA) subscales.

2.6. ROC analysis

For each participant separately, we calculated ROCs for neutral-neutral, neutral-positive and neutral-negative pairs using the confidence judgments for old items (hit rates) and new items (false alarm rates) for the item ROCs, and for old pairs (hit rates) and recombined pairs (false alarm rates) for the associative ROCs. Using the excel solver function (Dodson, Prinzmetal, & Shimamura, 1998), we estimated parameters for familiarity (d′) and recollection (Ro) for the item recognition task, and for familiarity (d′), recollection of old pairs (Ro) and recollection of new pairs (Rn) for the associative recognition task. The area under the curve (AUC) was used as a measure of overall recognition performance.

2.7. EEG recording and analysis

The EEG was recorded from 28 Ag/AgCl electrodes embedded in an elastic cap according to the extended 10/20 electrode system. Horizontal EOG activity was captured with electrodes placed at the outer canthus of each eye, and vertical EOG activity was captured by two electrodes placed above and below the right eye, respectively. The signal was amplified from DC to 250 Hz using BrainAmp (Brain Products, Inc.) DC amplifiers and digitized at a rate of 500 Hz. The EEG was on-line referenced to the left mastoid electrode and grounded to AFz. Due to equipment failure, the EEG was not recorded for one participant in the control condition, resulting in 18 participants in each group in the main EEG analysis.

The data were processed off-line using BrainVision Analyzer 2.0. The EEG was re-referenced to linked mastoids, high pass filtered with a cutoff frequency of 0.05 Hz, and notch filtered at 50 Hz. Next, segments of −300 ms to 1900 ms respective to the onset of the second word of each pair were extracted. The onset of the second word was chosen, because item memory was tested for the second word only, and because upon onset of the second word, both an associative and an item trace could be formed. Eye blinks and horizontal saccades were removed from the segmented EEG by applying the semi-automatic ICA-based ocular correction implemented in BrainVision Analyzer. Subsequently, we applied a 30 Hz low-pass filter. Segments containing residual artifacts were semi-automatically rejected. First, segments were marked as artifactual if they contained steps of 50 μV within 1 ms or if the maximal amplitude difference within the segment exceeded 70 μV. In addition, an expert who was blind to the group the participant was in and to the stimulus type of a given segment manually screened for residual artifacts. Separate ERP averages for neutral, negative and positive words were then calculated using only artifact-free trials. The mean trial numbers included were: control group: neutral: 48.17, positive: 48.22, negative: 47.22; stress group: neutral: 52.39, positive: 52.44, negative: 52.06. The subject ERP averages were baseline corrected using the mean amplitude in the 300 ms time window before word onset. We analyzed mean amplitudes from the slow wave time window (1000–1900 ms after word onset, which is a typical time window for the frontal slow wave to be maximal) for a 3 by 3 electrode grid including F3, Fz, F4, C3, Cz, C4, P3, Pz and P4.

To analyze SMEs, separate ERP averages within each valence type were calculated for words that had subsequently received a "definitely old", "probably old" or "maybe old" judgment ("subsequently remembered"), and for words that had received a "definitely new", "probably new" or "maybe new" judgment ("subsequently forgotten") in the item recognition test. The focus of the SME analysis on the item test had two rationales. First, the behavioral data showed a stress-related increase in item memory only. Secondly, dividing the encoding trials by the retrieval success in the associative test would have allowed for the inclusion of only pairs that were tested in their intact pairing. This would have resulted in much smaller trial numbers, in turn leading to the exclusion of more participants from the SME analysis. In the analysis of the SMEs related to item-encoding, data from three participants with less than 8 artifact-free trials in one of the six resulting ERP categories were excluded, resulting in 16 participants in the control group and 17 participants in the stress group.

2.8. Statistical analysis

We statistically analyzed all dependent variables in mixed ANOVAs, which were Greenhouse-Geisser corrected where necessary, using IBM SPSS 24 software. We report partial eta squared (η_p^2) as a measure of effect size. Significant main effects of factors with more than one level and interactions were followed up by lower-level ANOVAs and t-tests. P-values of follow-up tests for which we had directed *a priori* hypotheses were not corrected for multiple comparisons.

3. Results

3.1. Stress response

3.1.1. Cortisol

The cortisol measures (Fig. 2A) were entered into a 6 (Time Point)

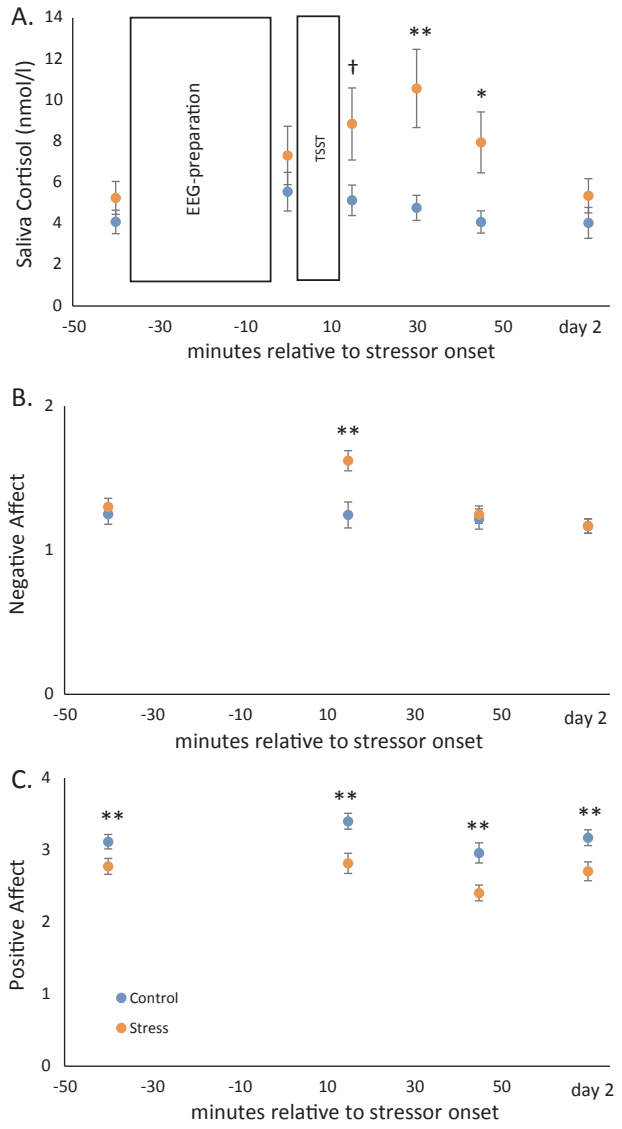

Fig. 2. Saliva cortisol levels (A) and PANAS values (B) for all measurement time points. The time points are (1) after signing the informed consent form (−40 min respective to the onset of the TSST/fTSST), (2) after the preparation of the EEG / immediately before the TSST/fTSST (0 min), (3) immediately after completion of the TSST/fTSST (+15 min), (4) during the second break of the encoding task (+30 min), (5) after the encoding task (+45 min) and (6) upon arrival in the laboratory on day 2.

by 2 (Group) mixed ANOVA. There was a significant main effect for Time Point, $F(2.54, 88.71) = 7.06$, $p = .001$, $\eta_p^2 = 0.168$, which was qualified by an interaction, $F(2.54, 88.71) = 4.02$, $p = .014$, $\eta_p^2 = 0.103$. There was no difference in saliva cortisol between the two groups before the stress manipulation (time points 1 and 2) or on day 2 (time point 6; all p-values $> .24$). The group difference approached significance for time point 3, $t(35) = 1.92$, $p = .063$, and was statistically significant for time points 4, $t(35) = 2.84$, $p = .007$, and 5, $t(35) = 2.40$, $p = .022$, reflecting the larger saliva cortisol level in the stress group.

3.1.2. PANAS

A 4 (Time Point) by 2 (Group) mixed ANOVA on negative affect (NA; Fig. 2B) revealed a significant effect for Time Point, $F(2.46, 86.05) = 11.99$, $p = .000$, $\eta_p^2 = 0.255$, which was qualified by a Time Point by Group interaction, $F(2.46, 86.05) = 7.25$, $p = .001$, $\eta_p^2 = 0.172$. Participants in the stress group reported stronger NA than those in the control group only at time point 3, that is, immediately after the stress manipulation.

For PA, there was a main effect for Time Point, $F(2.49, 87.18) = 9.69$, $p = .000$, $\eta_p^2 = 0.217$, and a main effect for Group, $F(1, 35) = 12.31$, $p = .001$, $\eta_p^2 = 0.26$, but no interaction ($p > .43$). The control group exhibited higher positive affect than the stress group at all time points.

3.2. Behavioral results

The empirical ROC curves for the group-level data, for each group, pair type, and recognition test are shown in Fig. 3A. Fig. 3B shows the area under the curve (AUC) as a measure of overall recognition performance, and Fig. 3C shows familiarity and recollection parameters for the item test, which were estimated for each subject separately. We analyzed each parameter in 3 (Emotionality) by 2 (Group) mixed ANOVAs.

3.2.1. Overall item and associative recognition performance (AUC)

Compared to the control group, the AUC for the item test was numerically higher in the stress group for positive and neutral items, but showed the reverse pattern for negative items (Fig. 3B). This differential effect of stress on item recognition for the different valences was confirmed by a significant interaction between Emotionality and Group, $F(1.59, 55.58) = 4.64$, $p = .02$, $\eta_p^2 = 0.117$. The main effect for Emotionality was also significant, $F(1.59, 55.58) = 7.28$, $p = .003$, $\eta_p^2 = 0.172$, reflecting an unexpected overall tendency for recognition memory to be more accurate for neutral than emotional words. Independent samples t-tests comparing item memory between the two groups for each valence category revealed a significant enhancing effect of pre-learning stress on recognition performance only for the positive words, $t(35) = 2.22$, $p = .033$ (negative and neutral words: both p-values $> .28$).

The ANOVA on associative AUC (Fig. 3B) did not reveal any main effects or interactions (all p-values $> .18$).

3.2.2. Item familiarity (d') and recollection

The ANOVA on the familiarity parameter (d') did not reveal any main effects (both p-values $> .14$), but a significant interaction between both factors, $F(1.53, 53.49) = 4.05$, $p = .033$, $\eta_p^2 = 0.104$. For the negative words, familiarity was numerically lower in the stress, compared to the control group, but this difference was not significant ($p > .37$). For the neutral and positive words, the stress group showed a higher familiarity parameter than the control group. This difference was significant for the neutral words, $t(35) = 2.22$, $p = .033$, and approached significance for the positive words, $t(35) = 1.88$, $p = .069$.

The ANOVA on the recollection (Ro) parameter revealed a significant main effect for Emotionality, $F(2, 70) = 11.74$, $p < .001$, $\eta_p^2 = 0.251$, but no main effect for Group or interaction (both p-values $> .45$). A post-hoc series of 2 (Emotionality) by 2 (Group) ANOVAs on each pair of valences revealed significant differences in recollection between negative and neutral words, and between positive and neutral words (both p-values $< .001$), but no difference between positive and negative words ($p > .31$). Taken together, unexpectedly, neutral words were more likely to be recollected than positive and negative words, but this effect was not modulated by stress (Fig. 3C).

Since there were no effects or interactions on overall associative recognition (Section 3.2.1), the estimates of associative familiarity and recollection are not reported here.

3.3. Slow wave

Slow wave amplitudes (Fig. 4) were analyzed in 3 (Anteriority) by 3 (Laterality) by 3 (Emotionality) by 2 (Group) mixed ANOVAs. Due to the relevance to our hypotheses, we only report main effects or interactions involving the factors Emotionality or Group.

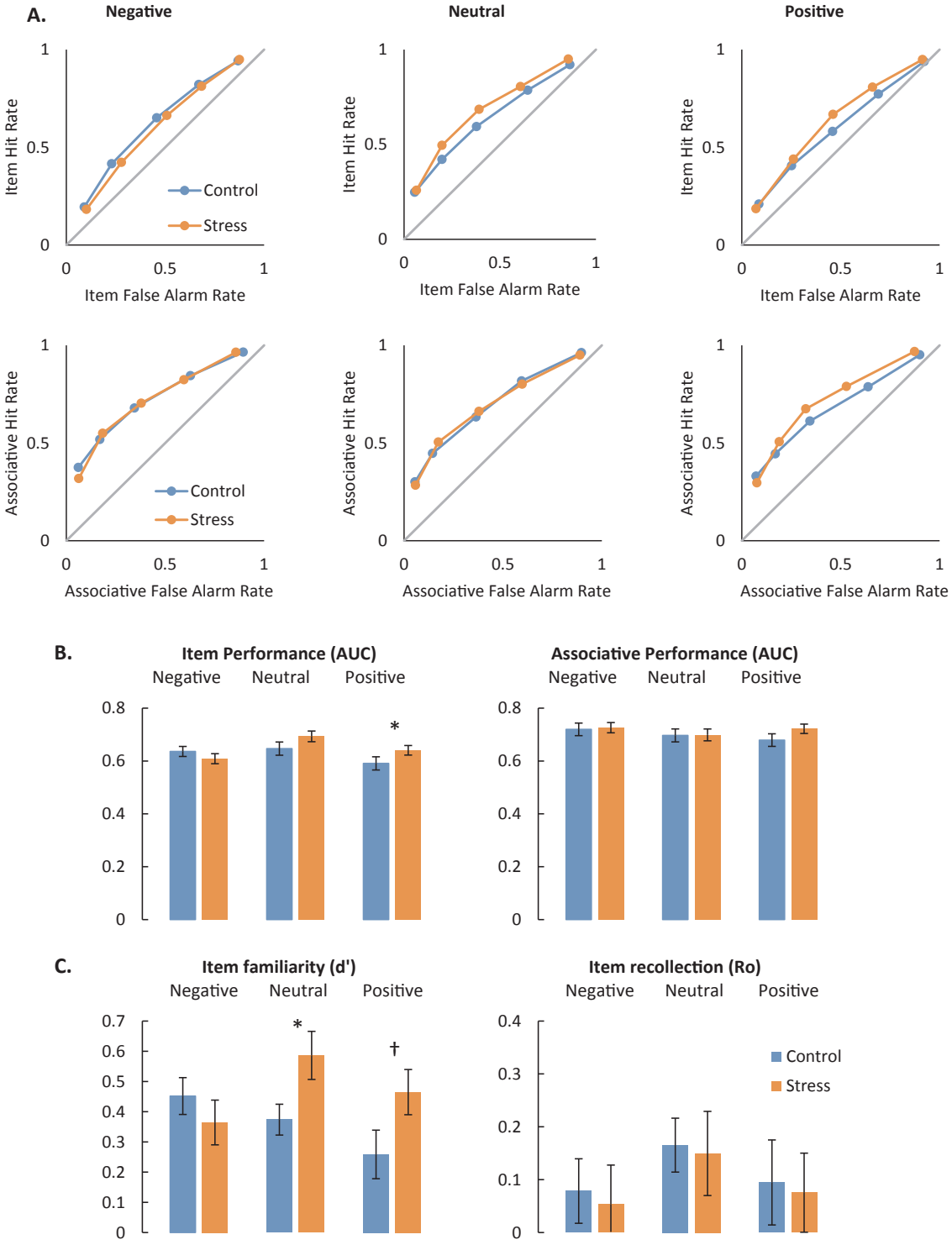

Fig. 3. Results from the ROC analysis of the item recognition test and the associative recognition test on day 2. A. Empirical ROC curves generated for illustration purposes on the group-level data, for both recognition tests and pairs of the three valence categories. B. Overall recognition performance, as estimated by the area under the curve (AUC). C. Familiarity and recollection parameters in the item test, for all three valence categories.

ERPs showed the biggest group differences in the midline electrodes. This was reflected in an interaction between Laterality and Group, $F(2, 68) = 4.02$, $p = .047$, $\eta_p^2 = 0.086$. The main effect for Emotionality, $F(2, 68) = 3.55$, $p = .034$, $\eta_p^2 = 0.094$, was qualified by interactions of this factor with Group, $F(2, 68) = 3.42$, $p = .039$, $\eta_p^2 = 0.091$, and with Anteriority, $F(2.48, 84.40) = 4.85$, $p = .001$, $\eta_p^2 = 0.125$.

In a follow-up analysis to the interaction between Emotionality and Group, we analyzed amplitude differences between the two groups for each level of emotionality at the midline electrodes in 3 (Anteriority) by 2 (Group) ANOVAs. For negative words, no main effects or interactions with the factor Group were present (both p-values $> .11$). For neutral words, there was a significant interaction between Anteriority and Group, $F(1.38, 46.99) = 3.91$, $p = .025$, $\eta_p^2 = 0.103$, reflecting a difference between groups at electrode Fz ($p < .018$), but not at Cz ($p = .055$) or Pz ($p > .77$). For the positive words, there was a main

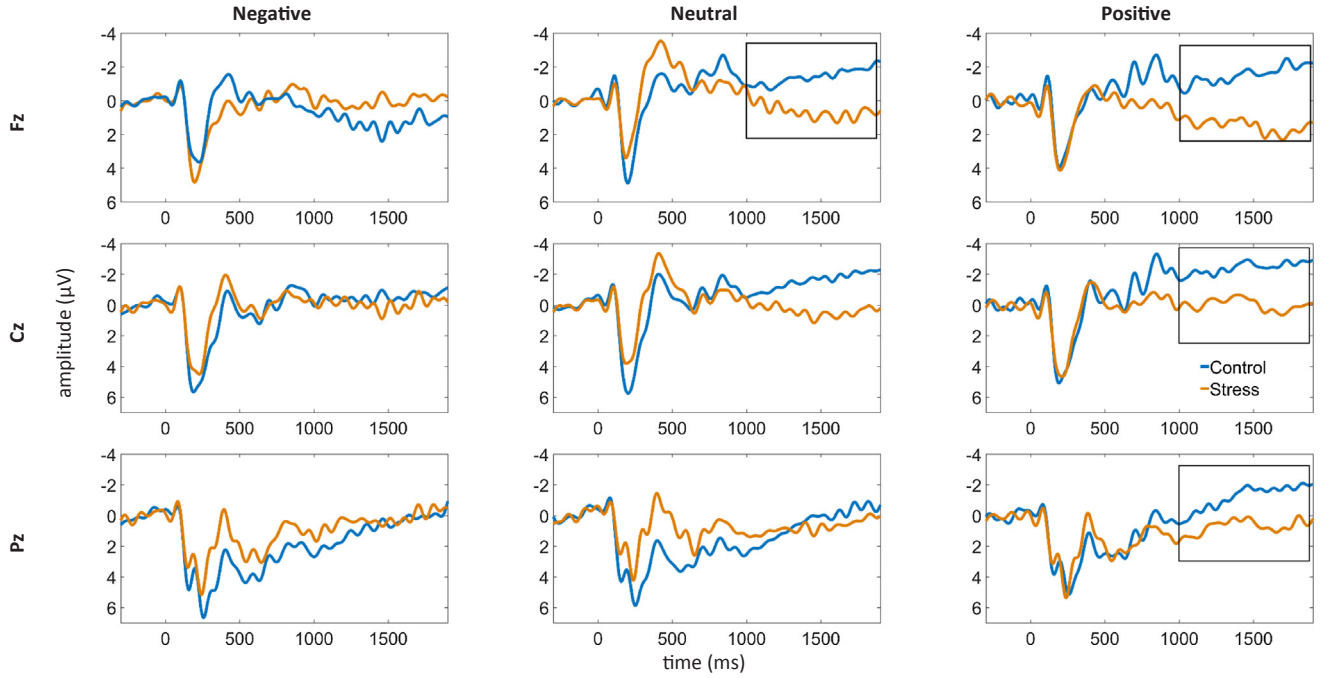

Fig. 4. ERPs elicited by the second word of a pair, depending on its valence for a frontal (Fz), a central (Cz) and a parietal (Pz) midline electrode. Frames indicate that the difference between the slow wave amplitudes elicited in the stress condition were significantly different from the amplitudes elicited in the control condition.

effect for Group ($p = .025$), but no interaction ($p > .25$). Taken together, pre-learning stress enhanced (in the positive direction) slow wave amplitudes for positive, and at frontal electrodes also for neutral, words. However, ERP slow waves elicited by negative words were unaffected by stress.

3.3.1. Subsequent memory analysis

Next, we analyzed slow wave amplitudes at Fz in a 3 (Emotionality) by 2 (Subsequent Memory) by 2 (Group) ANOVA (Fig. 5). The significant main effect for Subsequent Memory, $F(1, 31) = 6.32$, $p = .017$, $\eta_p^2 = 0.169$, was qualified by a three-way interaction, $F(2, 62) = 3.39$, $p = .04$, $\eta_p^2 = 0.098$. Paired samples t-test for the control group, comparing amplitudes for subsequent hits to subsequent misses for each emotionality separately, revealed no significant SMEs (although the difference approached significance for the negative and neutral words; both p-values $< .1$). By contrast, in the stress group, there was a significant SME for the positive, $t(16) = 3.18$, $p = .006$, but not for negative and neutral words (both p - values $> .33$).

Taken together, reliable slow wave SMEs were only found for positive words, and only in the stress group. We next examined whether cortisol after the manipulation (time points 3–5) was correlated with the magnitude of the SME, and indeed found such a correlation for positive words, $r(33) = 0.486$, $p = .004$. For neutral words, the correlation was not significant, $r(33) = 0.130$, $p > .47$, and for negative words, there was a non-significant tendency in a negative direction, $r(33) = -0.231$, $p > .19$ (Fig. 6).

4. Discussion

The present study investigated the effect of pre-learning psychosocial stress on subsequent item- vs. inter-item associative memory for positive, negative and neutral words. We found that item, but not

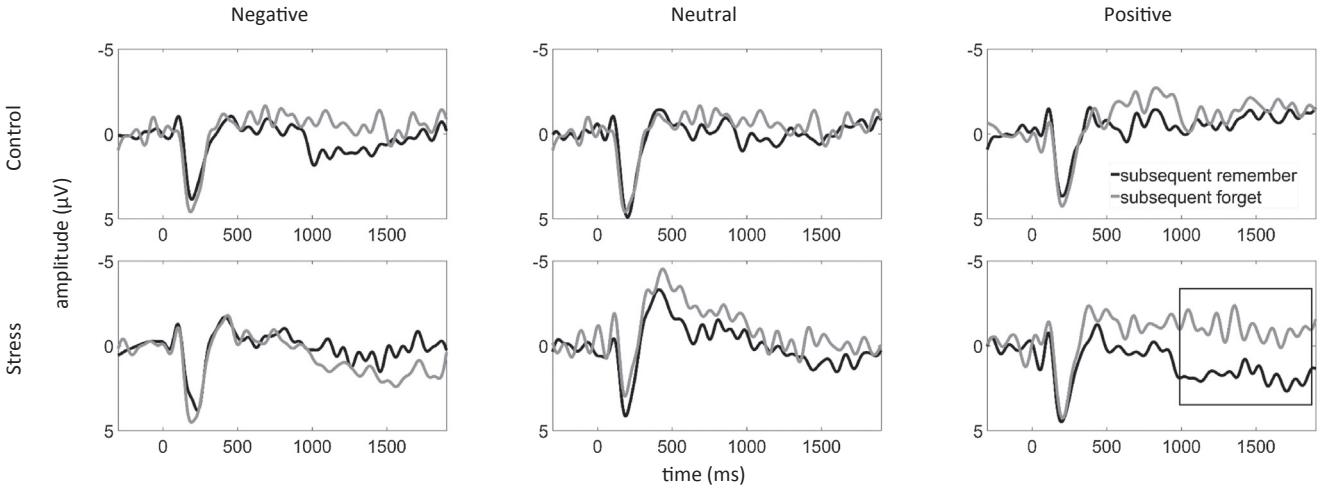

Fig. 5. ERPs at electrode Fz elicited by subsequently remembered (black line) and subsequently forgotten (grey line) words for both groups and for the three valence types. Basis for the subsequent memory distinction is performance in the item test. A frame indexes that the difference in slow wave amplitude between subsequently remembered items and subsequently forgotten items was statistically significant.

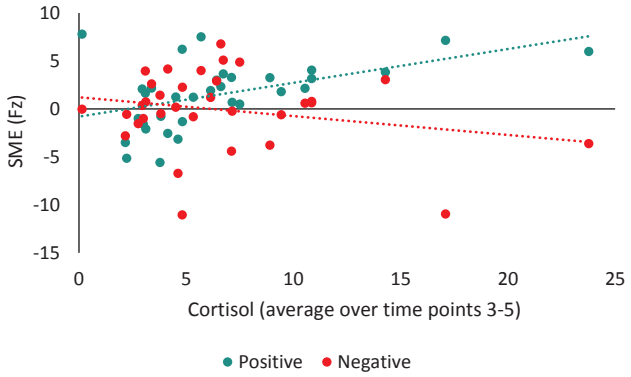

Fig. 6. Correlation between saliva cortisol after the TSST/fTSST and the frontal slow wave SME for positive and negative words. The correlation is statistically significant for the positive, but not for the negative words. See Section 3.3.1 for details.

associative, recognition for positive, but not negative words was enhanced due to pre-learning stress, likely due to an increase in familiarity-based retrieval. Furthermore, stress affected the amplitude of the frontal slow wave elicited by positive words. Finally, we found a frontal slow wave SME only for the positive words and only in the stress group, and this SME was correlated with the cortisol level. Taken together, our results suggest that pre-encoding stress affects neural processes related to episodic encoding of positively valenced verbal information and support the idea that stress can lead to a "boost" in episodic encoding for some kinds of stimulus material that is learned immediately after the experience of a psychosocial stressor. This timing appears to be crucial, because when a stressor is temporally separated from learning, previous studies have shown a reduction rather than an increase in subsequent memory (e.g., Zoladz et al., 2011).

4.1. A closer look at the behavioral results

Our behavioral results are somewhat inconsistent with Goldfarb et al. (in press), who reported, opposite to our findings for positive words, that pre-encoding stress improved memory for associations of negative-neutral pairs, but did not affect item memory. One possibility is that stress enhances item memory for positive information while it enhances associative memory for negative information; however, we did not observe a tendency in this direction for the neutral-negative pairs in our data. One reason for the discrepant findings could be differences in characteristics of the pre-encoding stress manipulation: Thus, while in our study the learning task immediately followed the stressor, Goldfarb et al. used a 19 min delay. Furthermore, Goldfarb et al. used the cold pressure test, while we employed the TSST. Notably, the cortisol response in Goldfarb et al.'s study was similar to the baseline level 30 min after the end of the stressor, while in our study, cortisol was still significantly elevated 30 min after stressor offset (that is, 45 min after stressor onset, see Fig. 2), supporting the idea that the stress manipulations differed in important ways. Similarly, there are also differences in the encoding task. While the interactive imagery instruction of Goldfarb et al. may have facilitated the creation of a unitized representation, our sentence generation task presumably kept each word a separate item within memory. It is possible that stress differentially affects these two types of associative tasks. Finally, another key difference between the studies is that we included only male participants while Goldfarb et al. included both genders. Clearly, more research is necessary to resolve these questions.

Other aspects of our behavioral results warrant some discussion. Thus, the generally higher associative, compared to item memory performance suggests that our paradigm prioritized encoding of associations over item-specific details. On the one hand, this may be due to the associative nature of the sentence generation task. On the other hand, one word of each pair was tested in the item test before the associative test. Although this feature of design did not differ between stress groups or valence categories and can therefore not account for our main findings, it is possible that during the item test, participants retrieved an old item's associate, thereby strengthening the associative memory trace. The order of the two memory tests could therefore have boosted associative memory across groups and valence categories, resulting in the general advantage of associative over item memory that we observed. The fact that we found stress effects on item memory although the paradigm exhibited a relative de-emphasis on item encoding provides additional confidence in the effect, but it also raises the alternative explanation that more difficult tasks (in our case, item memory) benefit from stress while easier tasks (associative memory) do not. Further research should therefore replicate our findings with a task that prioritizes item over associative encoding.

Also strikingly, episodic item memory was better and relied more strongly on recollection for neutral words, compared to negative and positive words in both groups. This unexpected pattern contradicts the typical finding of better memory for emotionally arousing stimuli (e.g., Kensinger, 2009). Perhaps distinctive encoding or retrieval of the positive and negative words was hindered by a higher semantic or thematic within-category similarity of the positive and negative, compared to the neutral words. In fact, due to the need for a sufficient number of trials in each word category (90 of each kind), we were unable to control for possible pre-existing differences in semantic cohesion or semantic similarity within the negative, neutral and positive word categories, respectively. Perhaps the neutral words were therefore easier to distinctly connect with preexisting semantic knowledge for neutral words, leading to memory traces that were easier to distinguish from new stimuli in the recognition test. To test this explanation, future studies should replicate our behavioral results with a reduced number of pairs in each category that are controlled for semantic cohesion within each emotion category. Furthermore, a future ERP study could include a controlled manipulation of semantic cohesion of neutral stimuli and examine whether similar result patterns emerge.

4.2. Effects of stress on memory encoding: physiological mechanisms

According to one idea, stress effects on memory consolidation are due to an interaction of glucocorticoids with NE in the amygdala, which in turn modulates activity in the hippocampus and other memory-related areas (Roozendaal et al., 2006). An important question is whether this model may account for pre-learning stress effects on encoding in paradigms like ours. At least to the extent that hippocampal activity should be upregulated after stress, our results do not suggest so, because neither recollection-based retrieval nor memory for inter-item associations, for which the hippocampus is crucial, were significantly affected by stress. As a cautionary note, it is, however, important to keep in mind that we did not directly measure hippocampal activity.

It is also worth noting that if an interaction between cortisol and NE was responsible for enhancement of episodic encoding due to pre-learning stress, this should be reflected in an amplification of a different ERP SME than we observed. Thus, a parietal SME, driven by the P300, is often observed when item details are encoded and subsequently retrieved (Kamp & Donchin, 2015; Kamp, Brumback, & Donchin, 2013; Karis et al., 1984). The P300 has been attributed to a phasic elevation of cortical NE release (Nieuwenhuis, Aston-Jones, & Cohen, 2005), and P300-like activity has been observed with intracranial recordings from the hippocampus (Axmacher et al., 2010). Taken together, if an interaction of cortisol with NE in the medial temporal lobe caused the memory boost, there should have been an amplified parietal SME in the stress group, but this is not what we observed.

An alternative physiological explanation is that glucocorticoids modulate dopaminergic activity in the prefrontal cortex (PFC), thereby impacting encoding. Interactions between the amygdala and the PFC have, indeed, been implicated in the effects of valence on memory

(Kensinger & Corkin, 2004). This idea is consistent with the modulation of frontal slow wave amplitude and SMEs due to the stressor and with the correlations of SMEs with cortisol levels observed in our study. The evidence is, however, only indirect, so this idea must be further tested.

4.3. Cognitive mechanisms not directly related to stress

In addition to interactions of HPA axis and SNS activation with encoding, there may be contributions from other, more "cognitive" mechanisms (see also Shields et al., 2017). For example, a stronger attentional focus on the positive words could reflect an affective "counter-regulation" mechanism (Rothermund, Voss, & Wentura, 2008). According to this idea, in order to flexibly regulate emotional states, attention tends to be drawn to information that is opposite in valence to what is currently experienced or anticipated. Extending this idea to our paradigm, attention may have been focused on the positively valenced words in order to counteract the negative affect caused by the stressor, which in turn could have enhanced memory for the positive words. Thus, modulation of the slow wave (SME) in response to positive words may reflect deeper, more elaborate processing of positive information to counteract the negative affect caused by the stressor.

Related to this idea, stress could lead to an internal semantic shift towards a positive "scheme" (opposite to the negative affect of the stressor), into which negative words were more difficult to integrate. The resulting facilitation of semantic processing of positive words could have boosted item encoding of positive words in the stress group. This idea is supported by the fact that 300–500 ms after the stimulus, the stress group exhibited a larger N400 at electrode Pz than the control group for negative and neutral words (Fig. 4; both *p-values* $< .05$), a difference that was not evident for positive words ($p > .23$). Since enhanced N400 amplitude indexes a relative difficulty of integration of verbal information into a semantic context (for a review, see Kutas & Federmeier, 2011), this supports the idea of a global semantic shift. Testing the explanatory power of the affective counter-regulation idea and related theories might be a fruitful route for future studies.

Another relevant view suggests that interactions between negative emotion and memory are due to a narrowed attentional focus on details, while interactions between positive emotion and memory are caused by more global factors like gist-processing (Kensinger, 2009). In line with this idea, Kamp, Potts, and Donchin (2015) reported that negative words were more likely to be recalled when they were encoded in isolation while positive words were recalled better when they were encoded in larger clusters. It is possible that in a paradigm like ours, with many words from each valence, stress amplifies the semantic cohesion effect presumably enhancing memory for positive words. Whether in a paradigm in which negative words are encoded in a more isolated manner, stress may also amplify encoding of negative words is an interesting question for future research.

Taken together, both effects of the physiological stress response and more general cognitive processes probably contributed to our result patterns. Either way, it is important to emphasize that relatively early neuro-cognitive encoding processes (within the first 2000 ms of stimulus presentation) that are unlikely to be affected by subsequent consolidation are affected by pre-learning stress, and that these processes are relevant for subsequent retrieval success. This conclusion cannot be reached based on behavioral measures alone, underlining the utility of recording ERPs in the context of the present research question.

4.4. Implications for the functional significance of ERP SMEs

We (Kamp et al., 2017) have proposed that the parietal SME reflects episodic encoding of item details, while the frontal slow wave SME is indicative of associative encoding. The findings of the present study do not completely support this suggestion. In line with other studies in which individual words were learned and tested (e.g., Bauch & Otten, 2012), we did not observe a parietal SME, even in a condition in which solely item information had to be subsequently retrieved. A modification of our proposal is based on the idea that when familiar words are learned, most of the item-specific details that are encoded are not actually part of the physical stimulus display, but rather come from entries in semantic memory and associations with previous knowledge. It appears that this kind of item-specific encoding is not reflected in the parietal SME. The parietal SME may occur only when encoding entails the bottom-up processing of distinctive item-specific features, such as physical or novel semantic features, and when subsequent retrieval relies on the reinstatement of such features.

We have also proposed that the frontal slow wave SME may reflect different kinds of associative processing, including item-to-item associations and item-to-context associations. Since encoding benefits from associative elaboration (Craik & Lockhart, 1972), the appearance of a frontal slow wave SME in our study is consistent with this proposal. However, future research should examine whether slow wave SMEs with different time courses or spatial distributions reflect elaborative processes involved in item vs. associative encoding. This appears likely, given that fMRI studies have implicated different PFC areas to be involved in episodic encoding of items and inter-item associations, respectively (e.g., Blumenfeld & Ranganath, 2006).

4.5. Limitations and conclusions

A limitation to our interpretation of differential stress effects on item vs. associative memory is the fact that numerically, associative memory of neutral-positive pairs also benefitted from pre-learning stress. It is possible that with an increase in power, a stress effect on associative memory for neutral-positive pairs may emerge. The dissociation of pre-learning stress effects on item- vs. associative memory should therefore be taken as a preliminary finding and be tested in additional studies.

Furthermore, there are some aspects of our study design that are somewhat unusual and may have affected the stress reaction. First, participants were informed of their assignment to the stress vs. control group already in the informed consent form, about 45 min before the stress induction. This detail is probably responsible for the fact that self-rated positive affect differed between the groups already before the stress induction (Fig. 2), and it is unclear how other aspects of the stress response or preceding expectations thereof may have been affected. Another aspect of our study that differed from others is that the experimenter who prepared the EEG-recording and led through the memory task was also part of the TSST-committee. Meeting the experimenter again on the second day could have cued another stress response during the memory test. Since memory retrieval is strongly affected by stress (Schwabe et al., 2012), this aspect of our design should be avoided in future studies. However, since stress negatively affects retrieval, whereas in the present study we found an enhancement of item recognition, it is unlikely to account for our results. If anything, our results may underestimate any true effect of stress on learning.

Finally, our sample included only men and are not necessarily generalizable to a female population. Future studies are necessary to explore potential gender differences of the effect of stress on encoding word pairs of different emotional contents.

The present study shows that, when experienced immediately before learning, stress can positively affect item encoding of positive words. Modulations of frontal slow waves appear to reflect the neurocognitive mechanisms underlying this effect during memory encoding. Correlations with cortisol suggest that the physiological stress response is one factor that contributes to this effect, but contributions from cognitive processes not directly related to the stress response, such as valence-specific attentional biases might also play a role. Future studies should explore whether the result patterns reported here can be extended to other kinds of stimulus material that is more similar to what

we may encounter in real life.

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