

# Stress Sensitizes the Brain: Increased Processing of Unpleasant Pictures after Exposure to Acute Stress

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## Abstract

■ A key component of acute stress is a surge in vigilance that enables a prioritized processing of highly salient information to promote the organism's survival. In this study, we investigated the neural effects of acute stress on emotional picture processing. ERPs were measured during a deep encoding task, in which 40 male participants categorized 50 unpleasant and 50 neutral pictures according to arousal and valence. Before picture encoding, participants were subjected either to the Socially Evaluated Cold Pressor Test (SECPT) or to a warm water control procedure. The exposure to the SECPT resulted in increased subjective and autonomic (heart rate and blood pressure) stress responses rela-

tive to the control condition. Viewing of unpleasant relative to neutral pictures evoked enhanced late positive potentials (LPPs) over centro-parietal scalp sites around 400 msec after picture onset. Prior exposure to acute stress selectively increased the LPPs for unpleasant pictures. Moreover, the LPP magnitude for unpleasant pictures following the SECPT was positively associated with incidental free recall performance 24 hr later. The present results suggest that acute stress sensitizes the brain for increased processing of cues in the environment, particularly priming the processing of unpleasant cues. This increased processing is related to later long-term memory performance. ■

## INTRODUCTION

Acute stressful events not only initiate a stress response in the body but also influence various types of cognitive functions, such as vigilance, attention, and memory. These responses in both the body and the brain are mediated by neurotransmitters, peptides, and hormones, such as catecholamines and glucocorticoids, affecting several brain areas, including the amygdala, the hippocampus, and the PFC (Joëls & Baram, 2009; Roozendaal, McEwen, & Chattarji, 2009).

Recent functional imaging findings indicate that acute stress is associated with increased activation of the amygdala and primary visual areas during processing of emotional stimuli, compared with the nonstress condition, suggesting that processing of significant stimuli in the environment is facilitated after acute stress (van Marle, Hermans, Qin, & Fernández, 2009; see also Henckens, Hermans, Pu, Joëls, & Fernández, 2009). Furthermore, increased coactivations between the amygdala and attentional networks (e.g., dorsal ACC and anterior insula) are observed in a resting state without experimental task after continuously watching highly stressful (vs. emotionally neutral) film clips (van Marle, Hermans, Qin, & Fernández, 2010). These results suggest that acute stress sensitizes the organism for prioritized

sensory processing of (threat-related) potentially significant information.

Furthermore, several studies suggest that acute stress also facilitates memory consolidation. Acute stress administered before or shortly after encoding of emotional pictures (Cahill, Gorski, & Le, 2003; Buchanan & Lovallo, 2001) results in enhanced long-term memory for these emotional events, indicating also a substantial role of emotional arousal on stress-mediated memory formation (Schwabe, Bohringer, Chatterjee, & Schachinger, 2008; Payne et al., 2007; Cahill et al., 2003; Buchanan & Lovallo, 2001; for reviews, see Schwabe, Wolf, & Oitzl, 2010; McGaugh, 2004). On the basis of these findings, acute stress seems to sensitize the facilitated processing of emotional stimuli and may also promote memory consolidation.

Previous ERP studies indicate that the processing of high-arousing emotional (pleasant and unpleasant) compared with low-arousing neutral stimuli evokes increased late positive potentials (LPPs) starting about 400 msec poststimulus over centro-parietal regions (Ferrari, Bradley, Codispoti, & Lang, 2011; Hajcak & Olvet, 2008; Codispoti, Ferrari, & Bradley, 2007; Schupp, Junghöfer, Weike, & Hamm, 2004; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; for a review, see Lang & Bradley, 2010). The LPP is particularly enhanced for pictures rated highest in emotional arousal and contents with high evolutionary significance (e.g., erotica and mutilated bodies; Schupp, Cuthbert, et al., 2004). A similar enlarged centro-parietal positive potential is observed during processing of target compared with

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nontarget stimuli also occurring between 300 and 700 msec, representing the P3, one of the most extensively explored ERP components in selective attention research. Accordingly, it has been suggested that, in addition to voluntary or instructed attention (attend to X and ignore Y), emotionally arousing pictures command for attentional resources and priority processing because of their intrinsic stimulus significance (Vuilleumier, 2005), a process that has been defined as “motivated attention” (Schupp, Cuthbert, et al., 2004; Lang, Bradley, & Cuthbert, 1997). In addition, the amplitude of the LPP is related to improved memory performance for pictures in later recognition tests (Dolcos & Cabeza, 2002; Palomba, Angrilli, & Mini, 1997), supporting the notion that the LPP reflects prioritized encoding of motivationally salient stimuli.

In the present experiment, we examined how imminent brief stress affects the encoding of emotionally significant and neutral stimuli using ERPs. Because the LPP is considered to reflect motivated selective attention processes, we expected the LPP to be specifically enhanced during encoding of emotional pictures following intensive stress exposure relative to the control condition. In addition, because of previous findings showing that the impact of stress on memory is modulated by emotional arousal (Cahill et al., 2003; Buchanan & Lovallo, 2001), we expected to find specific improvements of memory performance for emotional stimuli in the stressed participants (Payne et al., 2007). Moreover, based on the assumption that stress-induced sensitization during encoding might increase memory consolidation, we hypothesized that enhanced encoding-related activity revealed by the LPP predicted enhanced memory performance particularly for unpleasant pictures after acute stress.

## METHODS

### Participants

Forty healthy male students from the University of Greifswald (mean age = 24.5 years, range = 19–32 years, four left-handed; mean body mass index = 23.3 kg/m<sup>2</sup>, range = 19–26 kg/m<sup>2</sup>) participated in this study. Only male students were included to avoid any confounding sex effects on learning and memory processes (Cahill, 2006). Exclusion criteria were prechecked in a standardized telephone interview and included smoking, any medical condition within the prior 3 weeks, current or lifetime mental disorders, and current treatment with psychotropic medications, beta blockers, or steroids. Moreover, participants were asked to refrain from excessive exercise, meals, and caffeine within 2 hr before the experimental sessions. All participants had normal or corrected-to-normal vision. All participants provided informed written consent for the protocol approved by the ethics committee of the German Psychological Society and received financial compensation for participation.

### Stress Protocol and Control Condition

In a between-subject design, participants were randomly assigned to either the stress or control condition. Participants in the stress condition ( $n = 20$ ) were exposed to the Socially Evaluated Cold Pressor Test (SECPT) as described in detail elsewhere (Schwabe, Haddad, & Schachinger, 2008). Participants immersed their right hand up to and including the wrist for 3 min (or until they could no longer tolerate it) into ice water (0–2°C). During hand immersion, they were videotaped, asked to look into the camera, and told that these video recordings would later be analyzed for facial expression. Furthermore, participants were monitored by a rather cold and unsociable experimenter. The SECPT has been used in several studies as an efficient stress induction method that leads to significant elevations in autonomic arousal, salivary cortisol, and subjective stress ratings (Schwabe & Wolf, 2009, 2010; Schwabe, Böhringer, & Wolf, 2009).

In the control condition, participants ( $n = 20$ ) submerged their right hand up to and including the wrist for 3 min in warm water (35–37°C); they were neither videotaped nor monitored by an unfamiliar person. Subjective stress ratings and cardiovascular measures (heart rate and blood pressure) were collected to validate the efficacy of the SECPT.

### Subjective Stress Rating

Immediately after the SECPT or warm water control condition, participants indicated on a scale from 0 (*not at all*) to 100 (*very much*) how stressful, painful, and unpleasant the previous situation was experienced.

### Heart Rate and Blood Pressure Measurements

Heart rate and blood pressure were measured manually (Riva Rocci method) at three time points, immediately before (pre), during, and after (post) the SECPT or control condition.

### Stimulus Materials

Stimuli were taken from the International Affective Picture Series (IAPS; Lang, Bradley, & Cuthbert, 2008) based on their standard ratings for emotional valence and arousal. Two sets of stimuli were carefully matched according to their normative valence and arousal ratings of the standard sample for the encoding phase (see IAPS norms for male subjects; Encoding Set 1: mean valence = 3.0 and 5.3, mean arousal = 5.9 and 3.2, for unpleasant and neutral images, respectively; Encoding Set 2: mean valence = 3.0 and 5.1, mean arousal = 6.0 and 3.3). Moreover, both sets were matched for their semantic categories (e.g., human/animal attack, mutilation, neutral people, and objects). Each of the two picture sets consisted of 100 pictures

(50 unpleasant and 50 neutral pictures). Additionally, individual valence and arousal ratings of all pictures during encoding were obtained from the current sample to ensure that the ratings of the current sample corresponded to the reported IAPS norms. As expected, unpleasant pictures were rated as more unpleasant (mean valence = 2.9) than neutral pictures (mean valence = 6.4;  $F(1, 39) = 434.55, p < .001$ ). In addition, unpleasant pictures were rated as more arousing (mean arousal = 5.9) than neutral pictures (mean arousal = 2.5;  $F(1, 11) = 289.96, p < .001$ ). Valence and arousal ratings of the current samples did not differ between SECPT and control condition for unpleasant (valence:  $F(1, 19) = 3.07, p = .09$ ; arousal:  $F(1, 19) < 1$ ) and neutral (valence:  $F(1, 19) < 1$ ; arousal:  $F(1, 19) = 1.44, p = .24$ ) pictures.

### Procedure

All testing took place in the afternoon between 1 and 5 p.m. After a participant's arrival, preexperimental heart rate and blood pressure measurements were taken. Then, participants were exposed either to the SECPT or to the control condition in which heart rate and blood pressure were measured. Immediately thereafter, subjective assessments of the previous situation and heart rate and blood pressure were measured again. Twenty minutes after the SECPT/control treatment (before the picture encoding session started), heart rate and blood pressure measurements were taken again.

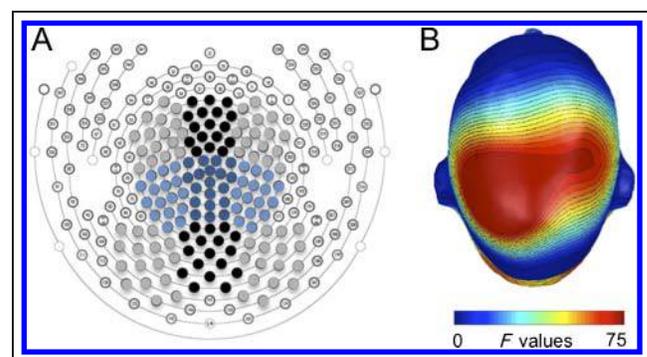
The picture encoding procedure was identical to a recent study from our laboratory (Weymar, Löw, Schwabe, & Hamm, 2010). During the encoding session, 100 pictures were presented for 3000 msec with a random inter-trial interval of 3500, 4000, or 4500 msec. A 500-msec fixation cross preceded each picture onset to ensure that participants fixated the center of the screen. Participants were instructed to attentively watch the pictures displayed on the monitor. Following picture offset, subjects were instructed to rate each picture on a keyboard according to arousal and valence using the Self-Assessment Manikin rating procedure (Bradley & Lang, 1994). Participants were not told that there would be a subsequent memory test. The pictures were presented in random order for each participant with the restriction that no picture from the same valence category was presented on more than three consecutive trials. The two sets of stimuli were counterbalanced across participants and both experimental groups. Before starting the encoding task, subjects were instructed to avoid eye blinks and body movements during ERP measurement.

Twenty-four hours after the encoding session, all participants completed a free recall test in the laboratory. They were instructed to write all pictures they could remember from the learning session on the day before within 15 min on a sheet of paper. As described in earlier studies (Dolcos & Cabeza, 2002), participants were instructed to provide enough details so that an outsider could identify each pic-

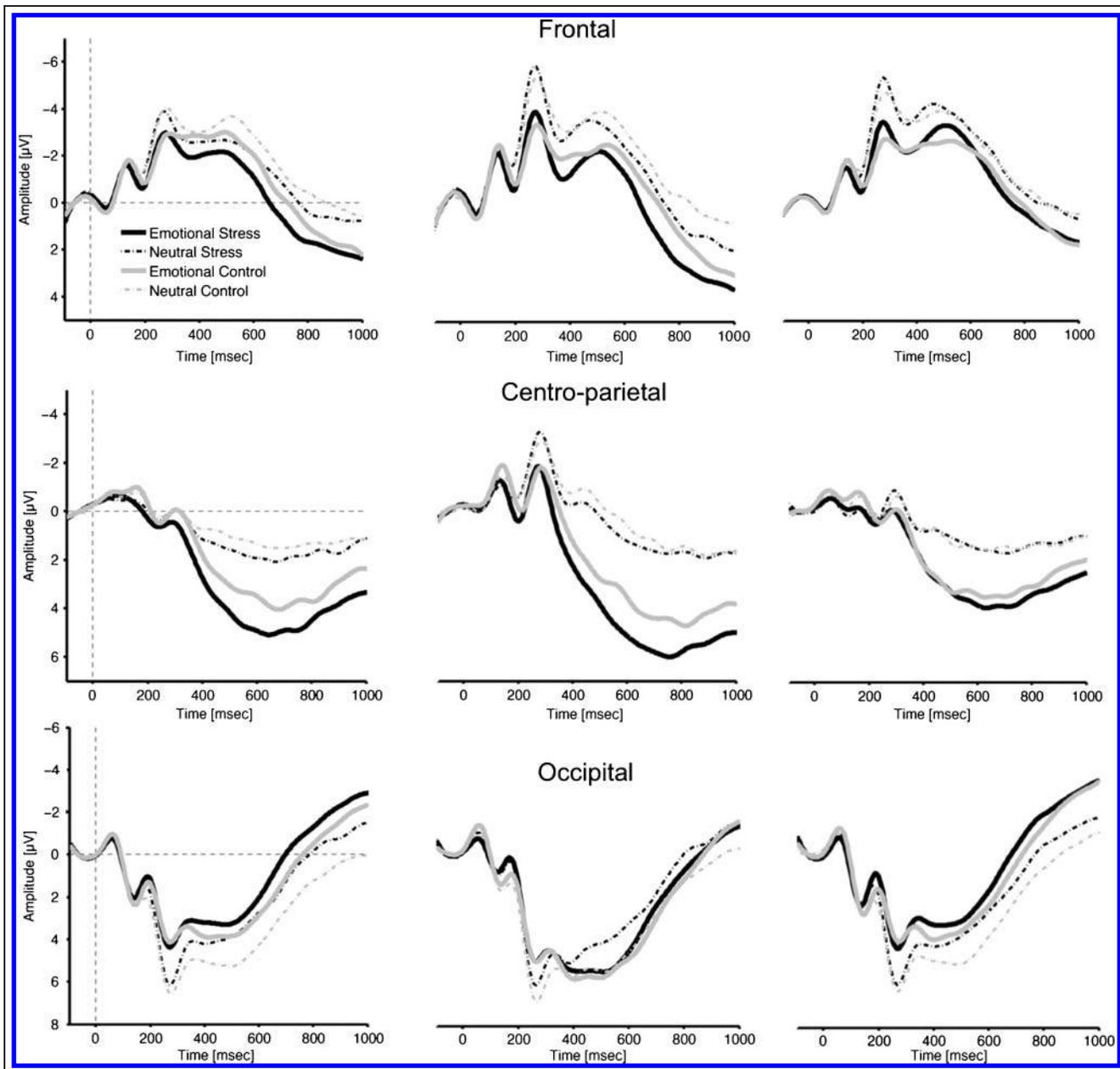
ture and discriminate it from similar pictures. Only pictures whose descriptions were detailed enough (e.g., human attack with knife vs. rifle) to allow both identification and differentiation were classified as remembered.

### Apparatus and Data Analysis

EEG signals were collected from the scalp using a 257-lead Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR). The EEG was recorded continuously with a sampling rate of 250 Hz with the vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 k $\Omega$ , as recommended by the manufacturer guidelines. All channels were band-pass filtered on-line from 0.1 to 100 Hz. Off-line analyses were performed using EMEGS (Junghöfer, Elbert, Tucker, & Rockstroh, 2000) including low-pass filtering at 40 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to the average reference. Stimulus-synchronized epochs were extracted from 100 msec before picture onset to 1200 msec after picture onset and baseline corrected (100 msec before stimulus onset). Finally, for each participant, separate ERP averages were calculated for each of the two picture categories for each sensor. To reveal effects of stress on emotional and neutral picture processing and to determine corresponding sensor clusters and time windows, visual inspection and single-sensor waveform analyses were used in concert. On the basis of visual inspection of the waveforms, statistical analysis was performed on the mean amplitude calculated in the window of 400–800 msec over centro-parietal regions (left and middle), where the overall LPP (see Figure 1B) and the stress effects on the LPP were maximum (see Figure 2). Mean ERP amplitudes (400–800 msec) of the centro-parietal sensor cluster were analyzed using an ANOVA including the factors Emotion (unpleasant vs. neutral) and Group (stress vs. control). For effects involving repeated measures, the Greenhouse–Geisser procedure was used to correct for violations of



**Figure 1.** (A) Display of nine predefined sensor clusters representative for frontal, centro-parietal, and occipital brain regions in the Geodesic Hydrocel Sensor Net diagram. (B) Illustration of the statistical main effect of emotion observed in the repeated-measures ANOVAs calculated for each sensor and mean interval (400–800 msec).



**Figure 2.** Grand-averaged ERP waveforms over nine scalp regions (clusters of sensors) for emotional (solid line) and neutral (dotted line) pictures following the stress exposure (black line) or the warm water control condition (gray line).

sphericity. In addition, ANOVAs containing the factors Emotion (unpleasant vs. neutral) and Group (stress vs. control) were calculated for each time point and separately for each individual sensor (Weymar, Löw, Melzig, & Hamm, 2009; Schupp, Junghöfer, et al., 2004) to confirm the inspection.

## RESULTS

### Subjective and Physiological Responses to Stress

Participants' subjective ratings and heart rate and blood pressure changes indicated that stress was successfully induced by the SECPT.

### Subjective Stress Ratings

As expected and shown in Table 1, participants of the SECPT group rated the hand immersion as significantly more stressful, painful, and unpleasant than participants in the warm water control group (stressful:  $F(1, 19) = 53.11, p < .001$ ; painful:  $F(1, 19) = 97.90, p < .001$ ; unpleasant:  $F(1, 19) = 61.67, p < .001$ ).

### Heart Rate and Blood Pressure

The SECPT exposure led to significant elevations in heart rate (Time  $\times$  Group,  $F(2, 76) = 7.72, p < .001$ )

**Table 1.** Subjective Stress Ratings and Blood Pressure Values before, during, and after the SECPT or Control Condition

	Control	Stress
<i>Subjective Assessments</i>		
Stressfulness	7.0 (2.1)	<b>56.0 (5.8)</b>
Painfulness	4.0 (2.2)	<b>66.0 (5.4)</b>
Unpleasantness	7.0 (2.6)	<b>64.0 (6.7)</b>
<i>Heart Rate (beats/min)</i>		
Before hand immersion	64.0 (2.5)	67.6 (2.1)
During hand immersion	61.6 (2.1)	<b>69.0 (2.2)*</b>
After hand immersion	61.4 (1.7)	60.4 (1.7)
<i>Systolic Blood Pressure (mmHg)</i>		
Before hand immersion	122.2 (0.5)	121.5 (0.9)
During hand immersion	120.7 (0.5)	<b>133.0 (1.3)</b>
After hand immersion	121.3 (0.7)	121.5 (1.1)
<i>Diastolic Blood Pressure</i>		
Before hand immersion	79.8 (0.7)	80.2 (0.6)
During hand immersion	79.4 (0.7)	<b>90.0 (0.6)</b>
After hand immersion	79.1 (0.7)	79.6 (0.7)

Stressfulness, painfulness, and unpleasantness were rated on a scale from 0 (*not at all*) to 100 (*very much*). Data in **bold font** indicate significant group differences ( $p < .001$ , \* $p < .05$ ). Data represent means and SEMs (in brackets).

and systolic (Time  $\times$  Group,  $F(2, 76) = 87.62$ ,  $p < .001$ ) and diastolic (Time  $\times$  Group,  $F(2, 76) = 107.26$ ,  $p < .001$ ) blood pressure relative to the control condition (see Table 1). During hand immersion, both groups differed in heart rate ( $F(1, 19) = 4.99$ ,  $p < .05$ ) and systolic ( $F(1, 19) = 68.92$ ,  $p < .001$ ) and diastolic blood pressure ( $F(1, 19) = 212.63$ ,

$p < .001$ ), whereas no differences were observed before hand immersion ( $F(1, 19) < 1$ ), supporting the view that the group differences were specifically evoked by the stress test rather than being a result of differences in overall physiological response level between groups.

### ERP Data

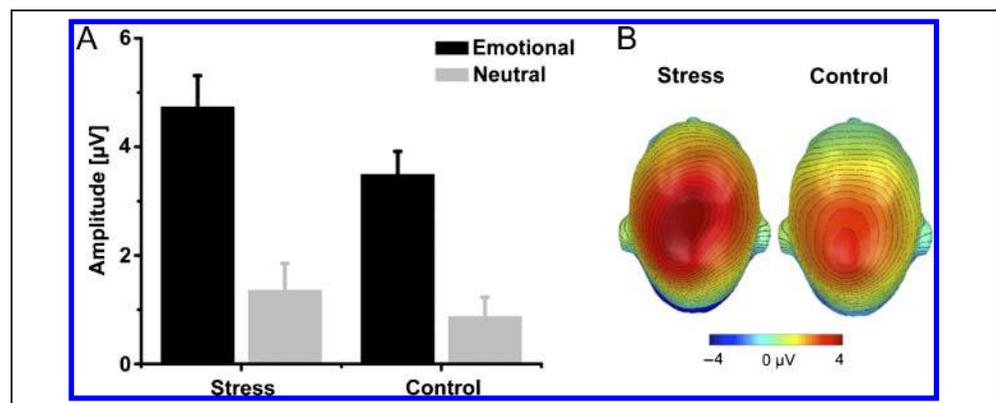
#### LPP (400–800 msec)

Figure 2 illustrates grand-averaged ERPs for unpleasant and neutral pictures for each experimental group (stress vs. control) averaged over nine sensor clusters (Figure 1A). On the basis of visual and statistical inspection, a 400–800 msec time window was selected over centro-parietal sensor clusters (left and central), in which the stress effects were maximum (see Figures 1B and 2). A main effect of Emotion was observed over centro-parietal sensor sites ( $F(1, 38) = 352.21$ ,  $p < .001$ ), showing increased LPPs during viewing of emotional compared with neutral pictures. Most interestingly, the LPP for unpleasant pictures was selectively modulated by stress as indicated by the interaction between emotion and group,  $F(1, 38) = 5.65$ ,  $p < .05$ . Follow-up tests revealed that the amplitude of the LPP was larger for unpleasant stimuli in the SECPT compared with the control condition ( $F(1, 19) = 4.43$ ,  $p < .05$ ) but not for neutral pictures ( $F(1, 19) = 2.36$ ,  $p = .36$ ), as shown by Figure 3A and B. Moreover, the Emotion effect in the LPP (unpleasant minus neutral) was significantly enhanced following the SECPT relative to the warm water control condition ( $F(1, 19) = 7.10$ ,  $p < .01$ ). A main effect of Group (SECPT vs. controls) was not observed,  $F(1, 38) = 1.78$ ,  $p = .19$ .

### Memory Data

Corroborating earlier findings (Dolcos & Cabeza, 2002; Bradley, Greenwald, Petry, & Lang, 1992), memory performance was affected by the emotional content of the pictures. Unpleasant pictures were better remembered than

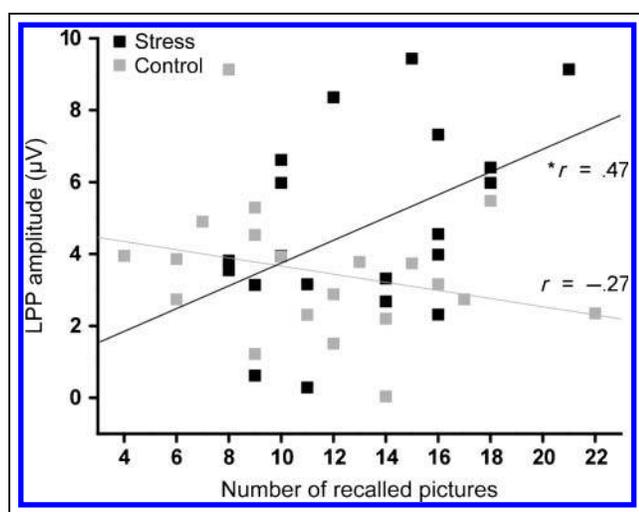
**Figure 3.** Neural correlates of enhanced emotion-specific encoding following exposure to acute stress. (A) The mean LPP amplitudes over the centro-parietal cluster during the time window from 400 to 800 msec are shown for emotional and neutral stimuli after acute stress (left) and after the control condition (right). (B) The scalp distribution of the ERP voltage difference (emotional – neutral) averaged across the 400–800 msec time window is shown separately for the two experimental groups (stress vs. control).



neutral pictures (proportions of recalled pictures: for unpleasant, .25 and for neutral, .10;  $F(1, 39) = 98.95, p < .001$ ). There were no main or interaction effects of Stress ( $F < 1$ ) on later memory performance. Interestingly, we obtained a significant correlation between the magnitude of the LPP during encoding of unpleasant pictures and the number of remembered unpleasant pictures in stressed participants (Pearson correlation  $r = .47, p < .05$ ) but not in the control group (Pearson correlation  $r = -.272, p = .25$ ; see Figure 4). On the other hand, no relationship between LPP amplitude and memory performance was found for neutral materials in the stress ( $r = .09, p = .69$ ) and control groups ( $r = .13, p = .59$ ). Using Fisher  $z$ -transformed correlations, the difference (emotional – neutral) of the LPP memory correlations differed between the stress and control groups ( $z = 2.42, p < .05$ ). Further comparisons revealed that, for emotional materials, correlations in the stress group were larger than in the control group ( $z = 2.31, p < .05$ ), but not for neutral stimuli ( $z = 0.09, p = .93$ ). Comparing these correlations for neutral and emotional materials within each group (Steiger, 1980) revealed no significant differences (stress group:  $z = -1.26, p = .21$ ; control group:  $z = 1.26, p = .21$ ).

## DISCUSSION

This study examined the influence of acute stress on the processing of emotional and neutral pictures using high-density ERPs. The viewing of emotional relative to neutral pictures induced larger LPPs, indexing enhanced motivational attention to these stimuli. Critically, the LPP for unpleasant pictures was affected by prior stress exposure,



**Figure 4.** Stress-induced enhanced encoding-related activity predicts subsequent memory for unpleasant pictures. Correlations between the mean 400–800 msec epoch LPP amplitude of unpleasant pictures recorded over a centro-parietal sensor cluster and the total number of remembered unpleasant pictures for both experimental groups (stress vs. controls).

resulting in stronger LPP amplitudes for unpleasant compared with neutral stimuli. This stress-induced modulation of brain activity during encoding was positively correlated with memory performance in a free recall task 24 hr later.

Previous work has indicated that stress facilitates learning and memory processes when stress is experienced in the context and around the timing of the learning episode, especially promoting the memory for highly salient emotional information (Diamond, Campbell, Park, Halonen, & Zoladz, 2007; Joëls, Pu, Wiegert, Oitzl, & Krugers, 2006). It has been suggested that stress promotes information processing via rapid nongenomic effects of catecholamines and glucocorticoids in the brain. In the current study, we could demonstrate—using ERPs—that the LPP during picture encoding is indeed enhanced by an exposure to stress before the task. Enlarged LPP amplitudes are well-known indices of selective attention processing to external cues (Nieuwenhuis, Aston-Jones, & Cohen, 2005). In addition, enhanced LPPs are found for emotional stimuli (e.g., Ferrari et al., 2008; Hajcak & Olvet, 2008; Schupp, Junghöfer, et al., 2004; Cuthbert et al., 2000), presumably reflecting increased attention allocation or elaborative processing because of their enhanced salience and motivational relevance (Lang & Bradley, 2010). The increased LPPs for unpleasant stimuli following the SECPT suggest that preexposure to stress leads to enhanced attention allocation toward these external cues. It has been suggested that stress particularly facilitates the encoding of emotional stimuli (Joëls et al., 2006). The current ERP results confirm this assumption. This finding clearly indicates that more processing resources are allocated to motivationally significant stimuli after acute stress. Known from fMRI and ERP studies, emotional picture viewing is linked to a distributed network including re-entrant connections between the amygdala and visual areas (Sabatinelli, Lang, Bradley, Costa, & Keil, 2009; Amaral, Price, Pitkanen, & Carmichael, 1992). Accordingly, perceptual processing in the visual cortex is amplified by input from the amygdala, and enhanced activations are observed in the amygdala and visual processing areas during and after stress (van Marle et al., 2009, 2010; Henckens et al., 2009). Comparing electrical and vascular brain activities during picture processing, it has been shown that LPP amplitudes are closely related to BOLD activity of the extrastriate visual cortex (Lang & Bradley, 2010; Sabatinelli, Lang, Keil, & Bradley, 2007). On the basis of the finding that the SECPT enhanced the LPP of the ERP activity to emotional stimuli, it may be speculated that stress enhances the hypervigilance toward external threat cues, hereby enhancing the (amygdala-mediated) elaborated perceptual processing in the extrastriate visual cortex. A possible physiological mediator underlying these stress effects may be linked to the enhanced activity of the locus coeruleus–norepinephrine system, which is coupled with amygdala activation under stress (Joëls & Baram, 2009; de Kloet, Joëls, & Holsboer, 2005).

In addition to enhanced encoding for emotional pictures after stress, we found that enhanced LPPs for unpleasant pictures were associated with later memory performance (Dolcos & Cabeza, 2002; Palomba et al., 1997) in participants exposed to the stressor. Recent animal and human studies indicate that stress facilitates memory consolidation (Schwabe et al., 2010; Roozendaal et al., 2009). Interestingly, although we did not find overall effects of stress on memory performance, enhanced attention allocation toward unpleasant material under stress was associated with subsequent memory. No such relationship was obtained for the control group or nonemotional pictures. These data are in line with animal studies showing that preexposure to stress sensitizes fear conditioning, such that low-intense stressors can produce robust fear behaviors (Rodrigues, LeDoux, & Sapolsky, 2009), which may help to explain why individuals with posttraumatic stress disorder (PTSD) react strongly to mild stimuli and quickly form new fears. Indeed, PTSD patients show increased P3 amplitudes to trauma-related stimuli (Karl, Malta, & Maercker, 2006). The data of the current study show that preexposure to acute stress particularly sensitizes the encoding of upcoming unpleasant stimuli. This sensitivity toward aversive cues may then facilitate the consolidation of aversive emotional memories. At least, the relationship we found between the brain activity during encoding and memory performance would be in line with such a hypothesis. Enhanced encoding and elaborative perception of unpleasant external cues after exposure to stress, as indicated by the current study, may be an important mechanism that drives the overconsolidation of traumatic memories and the development of PTSD.

Finally, three limitations of our study have to be addressed. First, we included only male participants to avoid the confounding effects of sex hormones on encoding and memory processes. Future studies are needed to investigate whether the current findings can be replicated in women. Furthermore, we specifically used negative arousing pictures as emotional stimuli. Therefore, we do not know whether the current stress effects on LPPs were driven by emotional arousal or were because of stimulus valence. A future study could test this by introducing positive arousing pictures. Finally, because we used a deep encoding task where participants explicitly directed their attention to emotional and neutral pictures to rate the emotional impact (valence and arousal), it is unclear whether the observed stress effects on LPPs can be replicated in a standard picture-viewing paradigm. This should also be addressed in future studies.

To summarize, in this study, we investigated the effect of acute stress on the neural activity during encoding of emotional pictures. We showed that acute psychosocial stress enhances LPPs in the ERPs, particularly during encoding of unpleasant stimuli, suggesting more elaborate perceptual processing of motivationally significant stimuli in response to stress. Moreover, the enhancement in LPP amplitudes was correlated with subsequent memory per-

formance. These findings provide neural evidence that stress facilitates motivated attention to emotionally relevant stimuli, resulting in enhanced mnemonic processing.

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