Emotional Memories are Resilient to Time: Evidence from the Parietal ERP Old/New Effect

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Abstract: Emotional memories can be extremely robust and long-lasting and can contribute to the development of anxiety disorders. Despite tremendous work on neural responses underlying the memory formation of emotional events, less is known about long-term retention. In the present study, behavioral and electrophysiological measures were used to investigate long-term recognition memory for emotional (unpleasant and pleasant) and neutral pictures after two retention intervals (1 week vs. 1 year) in 21 male subjects. The results show enhanced recognition performance for emotional relative to neutral pictures for both test delays. On the neural side, the retrieval of emotional pictures compared to neutral pictures was accompanied after 1 week by an enhanced old/new effect (500–800 ms), originating in the parietal cortex. After 1-year retention delay, only unpleasant but not pleasant pictures were different from neutral pictures in the recollection-sensitive ERP component. Analysis of the subjective awareness (confidence ratings) during recognition indicated that behavioral and electrocortical response patterns were exclusively driven by high confidence responses, an indication for recollection-based recognition. These results suggest that high arousing emotional memories were highly consistent over time relative to neutral memories. *Hum Brain Mapp* 32:632–640, 2011. © 2010 Wiley-Liss, Inc.

Key words: emotion; long-term memory; episodic memory; ERP old/new effect; parietal cortex

INTRODUCTION

Numerous studies have demonstrated that emotionally arousing events are better remembered than experiences without emotional relevance [McGaugh, 2004]. In most of these studies, memory performance was assessed either immediately after the encoding period or after a retention interval of weeks or several months [Anderson et al., 2006; Ochsner, 2000; Ritchey et al., 2008; Sterpenich et al., 2009; Weymar et al., 2009]. Only two studies assessed the mem-

ory-enhancing effect of emotions using longer retention intervals up to 1 year. Bradley et al. [1992] found a significantly higher memory performance of highly arousing unpleasant and pleasant emotional pictures compared to low arousing neutral pictures in a free recall task ~1 year after the encoding phase. Confirming these results, Dolcos et al. [2005] found increased recognition memory for emotional relative to neutral pictures after 1 year. In this study, participants also pressed a “remember” button to indicate that their memory performance was associated with recollection of some details of the picture or a “know” button to indicate the belief that they have seen the picture before without recollecting any details. Interestingly, improved long-term retrieval for emotional relative to neutral pictures was only observed for those stimuli that were associated with recollection-based memory processes and not for those stimuli that were recognized based on familiarity. Moreover, enhanced retrieval of emotional stimuli was associated with increased activation in the medial temporal lobe including the amygdala and the hippocampus, especially for recollection-based retrieval processes. The current study follows up on this research

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investigating the temporal dynamics of the neuronal correlates of the emotional modulation of long-term memory performance using high-density EEG recordings of event-related potentials (ERPs).

In general, when measuring ERPs during a recognition task, there is an enhanced positive deflection for correctly remembered “old” items compared to correctly classified “new” items. This old/new effect is reflected by two different spatiotemporal and functionally distinct components: An early frontally located old/new effect (also labeled as FN400; see Curran and Cleary [2003]) occurs between 300 and 500 ms and is believed to be sensitive to implicit memory processes based on familiarity (however see Voss and Paller [2008] for an alternative explanation). This early component can be separated from a later parietal old/new effect (>500 ms) which is considered to be the neural correlate of explicit recollection (for reviews, see Friedman and Johnson [2000] and Rugg and Curran [2007]). The neural generators of the parietal old/new effect are related to hippocampus [Düzel et al., 2001] and parietal cortex [Vilberg and Rugg, 2009], regions which were most frequently activated during episodic-memory retrieval in imaging studies [Cabeza et al., 2008; Olson and Berryhill, 2009; Wagner et al., 2005].

Recent research has demonstrated that the late parietal old/new effect is modulated when emotional contents are remembered. The late parietal old/new effect (>500 ms) is enhanced during retrieval of unpleasant and pleasant stimuli in immediate [Dietrich et al., 2001; Langeslag and van Strien, 2008] and intermediate retrieval following a 1-week retention interval [Weymar et al., 2009, 2010]. However, in some studies, the ERP old/new effect is more pronounced for unpleasant items than pleasant items [Inaba et al., 2005; Johansson et al., 2004]. This later component of the old/new effect is generally stronger for those stimuli for which the individuals either report higher recognition confidence or are sure that they *remember* these stimuli [Curran and Friedman, 2004; Duarte et al., 2004; Düzel et al., 1997; Weymar et al., 2009], suggesting that the increased late parietal old/new effect for emotional stimuli indexes explicit recollection-based memory processes.

In the present study, we measured event-related potentials using high-density recordings to investigate recognition memory for emotional and neutral pictures after an intermediate and a long retention interval (1-week vs. 1-year delay). A subsample of the participants of our previous study [Weymar et al., 2010] was reinvited to the laboratory for an additional recognition session ~1 year later. Recollection-based memory performance was assessed by collecting confidence ratings following each recognition judgment. Accordingly, high-confidence ratings should reflect the process of recollection [Wixted and Stretch, 2004; Yonelinas, 2001, 2002]. We were specifically interested whether the increased parietal ERP old/new effect for emotional pictures would be stable across longer retention periods and whether this modulation is especially driven by high-confidence responses indexing the recollection-based memory process.

METHODS

Participants

Twenty-one healthy male students from the University of Greifswald (mean age: 24.0 years, range: 19–31 years, one left-handed) participated in the study.¹ All had normal or corrected-to-normal vision. All participants provided informed written consent for the protocol approved by the Review Board of the University of Greifswald and received financial compensation for participation.

Stimulus Materials

Stimulus materials consisted of photographs taken from the International Affective Picture Series [IAPS; Lang et al., 2008].² Stimuli included pleasant (erotic couples, happy families, adventure, and sport scenes), unpleasant (mutilations, threat, and attack), and neutral (nature scenes, buildings, and neutral people) pictures. Three sets of stimuli (encoding set vs. recognition set 1 vs. recognition set 2) were carefully matched according to valence and arousal ratings of the standard sample [see IAPS norms for male subjects; Lang et al., 2008] and also according to their semantic categories. All three picture sets consisted of 90 unique pictures each (30 pleasant, neutral, and unpleasant pictures, respectively). Additionally, valence and arousal ratings of the 90 encoding pictures were obtained from the current sample after recognition 1 (1 week later) to ensure that the ratings of the current sample corresponded to reported IAPS norms. As expected, valence ratings corresponded to the ratings of the standard sample, and unpleasant and pleasant pictures were rated as significantly more arousing than neutral pictures [$F(1, 45) = 642.72, P < 0.001$]. In contrast to the standard sample, unpleasant pictures were rated as more arousing in the current sample than pleasant pictures [mean arousal ratings for pleasant ($M = 5.0$) and unpleasant ($M = 6.0$) pictures; $F(1, 45) = 60.28, P < 0.001$]. Forty-two pictures in the incidental encoding session served as buffer of which 21 pictures were presented at the beginning and 21 at the end of the sets to avoid serial position effects. These buffer pictures were not included in the analyses.

Procedure

The study consisted of three study sessions. EEG was measured during encoding, during retrieval after 1 week,

¹Subjects were a subsample of a previous study [Weymar et al., 2010].

²Nine erotic pictures were added from a picture set taken from Stark et al. [2005]. Normative ratings of these pictures were produced by male subjects and were included in the calculation of the overall means in valence and arousal of the pleasant pictures. Ratings were obtained using the Self-Assessment Manikin [SAM; Bradley and Lang, 1994].

and during retrieval after ~1 year (range, 10–15 months; mean, 11 months).

Encoding

During the incidental encoding session, 90 pictures were presented for 3,000 ms with a random intertrial interval (ITI) of 3,500, 4,000, or 4,500 ms. A 500-ms 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. No mention of a memory test was made. The pictures were presented in random order for each participant with the restriction that no picture from the same valence category was presented on two consecutive trials.

Recognition 1

One week after the encoding session, participants went through a recognition test, during which 90 old pictures were presented, randomly intermixed with 90 new pictures. Before starting the recognition task, subjects were instructed to avoid eye blinks and body movements during ERP measurement. Each picture was displayed for 3,000 ms with a preceding fixation cross of 500 ms. Following each picture, participants were asked to decide whether they had previously seen the picture and press either a “yes” or “no” button (old vs. new) and to indicate their recognition confidence on a Likert scale ranging from 0 (not confident) to 10 (absolutely confident). A keyboard was used to make responses. The assignment of left and right hand button presses to old and new responses was counterbalanced across retrieval sessions.

Recognition 2

All participants were invited again for a second recognition test ~1 year following their first participation.³ The methods were identical to recognition 1, except that 90 new pictures (recognition set 2) were randomly presented with 90 pictures from the initial encoding session.

Physiological Recording and Data Reduction

ERP data

EEG signals were recorded continuously from 256 electrodes using an Electrical Geodesic system and digitized at a rate of 250 Hz, using the vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 k Ω , as recommended by the manufacturer. All channels were bandpass-filtered online from 0.1 to 100 Hz. Continuous EEG data were low pass-filtered at 40 Hz using digital filtering before stimulus synchronized epochs from 100 ms

³Data from two subjects performing the recognition task after 1 week (recognition 1) were not reachable for the 1-year retention session (recognition 2) and were therefore excluded from the entire analyses.

before to 1,200 ms after picture onset were extracted and baseline-corrected (100 ms prior to stimulus onset). For data editing and artifact rejection, a two-step procedure was used for statistical control of artifacts, specifically tailored for the analysis of dense sensor recordings [Junghöfer et al., 2000; Junghöfer and Peyk, 2004]. The raw EEG epochs were first passed through a computerized artifact detection algorithm that uses statistical parameters (e.g., absolute value over time, standard deviation over time, etc.) to determine and reject channels and trials with artifacts. In a second step, based on the average referenced data, sensors containing artifact-contaminated activity were replaced using spherical interpolation on the basis of all remaining sensors for the given trial [Junghöfer et al., 2000].

Source analysis

To estimate the cortical distribution of the current source density that accounts for retrieval-related ERPs, we used the sLORETA algorithm [Pascual-Marqui, 2002] as implemented in the Brain Electromagnetic Source Analysis (BESA, version 5.2.4, MEGIS, Gräfelfing, Germany) software. The three-dimensional distribution of current source density was estimated with a four-shell ellipsoidal head model with a spatial resolution of 7 mm. sLORETA images represent the electric activity at each voxel as the standardized estimate of the current density. We obtained current source densities at each time point for the grand-averaged ERPs of each participant and each condition and averaged the current source density across the 500–800 ms time window over a parietal voxel cluster.

Statistical Analysis

Recognition accuracy (Pr as indexed by hit rates – false alarms rates), response bias Br [$p(\text{false alarm})/p(1 - \text{Pr})$], and confidence ratings taken as behavioral performance measures were analyzed using an ANOVA including the factors Emotion (pleasant vs. unpleasant vs. neutral) and Time (week vs. year).

Analysis of the distribution of the confidence ratings for the three stimulus categories revealed that correctly recognized pictures mainly received a confidence rating of 10 (51.4% of pictures during recognition 1; 27.4% during recognition 2)—for the rest of the pictures the confidence ratings steadily declined from 9 to 0. There is considerable evidence that familiarity-based responses increase gradually as function of recognition confidence, whereas recollection-based responses are primarily associated with the highest level of confidence [Wixted and Stretch, 2004; Yonelinas, 2001, 2002]. Therefore, we categorized those pictures receiving confidence ratings of 10 into the *high-confidence category* and all remaining pictures were assigned to the *low-confidence category*. The influence of confidence on memory accuracy (Pr) was analyzed by employing separate ANOVAs for high- and low-

TABLE I. Behavioral data

Picture type	Pr	Pr _{HC}	Pr _{LC}	Br	Confidence (old)	Confidence (new)
Unpleasant						
1-Week delay	0.70 (0.03)	0.64 (0.05)	0.06 (0.04)	0.76 (0.05)	9.13 (0.23)	7.37 (0.37)
1-Year delay	0.60 (0.04)	0.37 (0.05)	0.22 (0.04)	0.66 (0.06)	8.15 (0.26)	6.63 (0.32)
Neutral						
1-Week delay	0.49 (0.04)	0.36 (0.04)	0.13 (0.05)	0.55 (0.05)	7.92 (0.28)	6.69 (0.38)
1-Year delay	0.42 (0.03)	0.14 (0.03)	0.29 (0.03)	0.38 (0.05)	6.78 (0.35)	6.43 (0.26)
Pleasant						
1-Week delay	0.60 (0.04)	0.47 (0.05)	0.13 (0.05)	0.64 (0.06)	8.51 (0.24)	6.72 (0.38)
1-Year delay	0.52 (0.03)	0.22 (0.04)	0.30 (0.04)	0.53 (0.05)	7.34 (0.31)	6.15 (0.30)

Standard errors of the mean are given in parentheses.

Mean old–new discrimination (Pr) and Pr based on high confidence (HC) ratings and low confidence (LC) ratings for each picture type and test-delay, along with response bias (Br) and overall confidence ratings (confidence), are presented in the table.

confidence categories including the factors Emotion (unpleasant vs. neutral vs. pleasant) and Time (week vs. year).

Overall confidence ratings were analyzed with an ANOVA including the factors Memory (old vs. new), Emotion (unpleasant vs. neutral vs. pleasant), and Time (week vs. year).

ERP analyses were guided by previous work, showing that the late parietal old/new effect peaks within 500 and 800 ms after picture onset over parietal regions [Weymar et al., 2009, 2010; Wolk et al., 2006]. To determine the time course and topographical distribution for the late ERP old/new effect, visual inspection of the waveforms and analysis of variance (ANOVA) were applied in concert. Specifically, each time point and each individual sensor were tested separately in repeated-measures ANOVAs, including factors Emotion (unpleasant vs. neutral vs. pleasant), Memory (old vs. new), and Time (week vs. year). To control for spurious findings in the waveform analysis, we followed the algorithm applied in our previous work (see Schupp et al. [2003, 2007]). Significant effects were considered meaningful only when the effects were observed for at least eight continuous data points (32 ms) and two neighboring sensors [Schupp et al., 2007]. Based on the results of these analyses, we selected a time window from 500 to 800 ms and an electrode cluster over the centro-parietal cortex (see Fig. 2a) for further statistical analyses.

Mean ERP amplitudes (500–800 ms) of the centro-parietal sensor cluster were analyzed using an ANOVA including the factors Emotion (unpleasant vs. neutral vs. pleasant), Memory (old vs. new), and Time (week vs. year). The influence of confidence on recognition memory was analyzed by dividing the correctly memorized old pictures in those receiving high-confidence ratings (10) and those receiving low-confidence ratings (≤ 9). Mean ERP amplitudes of the 500–800 ms time window and centro-parietal cluster were analyzed with an ANOVA including the factors Emotion (unpleasant, neutral, pleasant), Confidence (old/confidence high vs. old/confidence low vs. new pictures) and Time (week vs. year). Statistical

analyses of the voxel clusters of the current source densities were analyzed with ANOVAs including the factors Emotion (unpleasant vs. neutral vs. pleasant), Memory (old vs. new), and Time (week vs. year). For effects involving repeated measures, the Greenhouse–Geisser procedure was used to correct for violations of sphericity.

RESULTS

Behavioral Data

An overview of the participants' recognition performance is given in Table I.

Discrimination accuracy and response bias

Replicating previous findings memory accuracy, as indexed by Pr, was modulated by picture content [$F(2, 40) = 24.36, P < 0.001, \epsilon = 0.80$]. Unpleasant and pleasant pictures were better discriminated than neutral pictures [unpleasant vs. neutral: $F(1, 41) = 46.42, P < 0.001$; pleasant vs. neutral: $F(1, 41) = 15.25, P < 0.001$]. Furthermore, discrimination accuracy for unpleasant pictures was better than for pleasant pictures [$F(1, 41) = 19.18, P < 0.001$]. In addition, there was a main effect of Time, suggesting that the old/new discrimination was reduced after 1 year relative to the 1-week delay [$F(1, 20) = 18.76, P < 0.001$]. This reduction was not significantly modulated by picture content [Emotion $\times$ Time: $F(2, 40) < 1$]. Analysis of the influence of confidence responses on memory performance showed that the enhanced memory for emotional pictures was driven by the high-confidence responses [Emotion: $F(2, 80) = 73.75, P < 0.001, \epsilon = 0.99$, unpleasant vs. neutral: $F(1, 41) = 123.81, P < 0.001$; pleasant vs. neutral: $F(1, 41) = 23.99, P < 0.001$, see Columns 2 and 3 in Table I]. If confidence was low, emotional modulation of memory performance was less pronounced and an opposite pattern of results was observed with lower discrimination accuracy for unpleasant pictures compared to pleasant [unpleasant vs. pleasant: $F(1, 41) = 8.31, P < 0.001$] and

Figure 1.

Recognition-test ERPs averaged across the parietal channel cluster are shown for correctly judged old and new items depicted separately for unpleasant, neutral, and pleasant pictures and retention interval (week vs. year). The shaded area represents the late (500–800 ms) time window used in the analyses. ERPs are aver-

aged across channels within the specific parietal cluster used in the analyses. The lower section shows the old/new effect (old minus new) of the mean amplitudes recorded over the centro-parietal cluster in the 500–800 ms time window separately for the three picture categories and retention interval (week vs. year).

neutral pictures [unpleasant vs. neutral: $F(1, 41) = 5.43$, $P < 0.05$]. Time did not interact with the type of confidence and memory discrimination accuracy [all $F(2, 80) < 1$].

The response bias (Br) also differed significantly between the three picture categories [Emotion: $F(2, 40) = 38.07$, $P < 0.001$, $\epsilon = 0.95$]. Emotional pictures were associated with a more liberal response bias than neutral pictures [unpleasant vs. neutral: $F(1, 41) = 82.26$, $P < 0.001$; pleasant vs. neutral: $F(1, 41) = 22.04$, $P < 0.001$]. Moreover, the probability of saying “yes” to an item was greater for unpleasant in comparison to pleasant pictures [$F(1, 41) = 17.75$, $P < 0.001$]. A main effect of Time [$F(1, 20) = 13.16$, $P < 0.001$] indicated that the liberal response bias decreased from 1 week to 1 year. No interaction was observed between picture category and test-delay [Emotion $\times$ Time: $F(2, 40) = 1.02$, $P = 0.36$].

Confidence ratings

Replicating previous findings, overall recognition confidence was higher for remembered old pictures compared to correctly classified new pictures [Memory: $F(1, 20) = 43.32$, $P < 0.001$]. As expected, emotional pictures were remembered with higher confidence in comparison to neutral pictures as suggested by a significant Emotion $\times$ Memory interaction [$F(2, 40) = 21.35$, $P < 0.001$, $\epsilon = 0.86$]. Moreover, confidence judgments decreased over time [Time: $F(1, 20) = 22.52$, $P < 0.001$] with lower ratings after the 1-year delay relative to the week delay. Additionally, a Memory $\times$ Time interaction was shown, indicating a decline in the confidence ratings for old pictures in the 1-year delay [$F(1, 20) = 6.49$, $P < 0.05$]. Emotion did not significantly influence these time-dependent recognition-related confidence judgments.

Figure 2.

(a) Geodesic Sensor net diagram: Marked electrodes represent the cluster used for ERP analysis. (b) Effects of Emotion on Memory. Illustration of the statistical interaction effects for the late parietal old/new effect observed in repeated-measures ANOVAs calculated for each sensor and mean time interval (500–800 ms).

ERP Data

Late parietal old/new effect: 500–800 ms

Figure 1 displays the ERP waveforms averaged across centro-parietal recording sites elicited by correct recognition and new responses for both retention delay conditions (week vs. year). Correctly classified old pictures were associated with a more positive ERP waveform than correctly rejected new pictures over parietal sensors [Memory: $F(1, 20) = 40.03, P < 0.001$]. This recollection-sensitive ERP difference was modulated by picture content [Emotion $\times$ Memory: $F(2, 40) = 10.34, P < 0.001, \epsilon = 0.90$]. Replicating previous findings, the old/new effect was significantly larger for the retrieval of emotional relative to neutral pictures over centro-parietal regions [unpleasant vs. neutral: $F(1, 20) = 19.78, P < 0.001$; pleasant vs. neutral: $F(1, 20) = 5.86, P < 0.05$] (see also Fig. 2). Moreover, the magnitude of the late parietal old/new effect was significantly larger for unpleasant relative to pleasant contents [$F(1, 20) = 5.03, P < 0.05$]. Retention interval did not influence these effects [Time: $F(1, 20) = 1.51, P = 0.23$; Memory $\times$ Time: $F(1, 20) < 1$; Emotion $\times$ Memory $\times$ Time: $F(1, 20) = 1.38, P = 0.26$]. After 1 week, the old/new effect during recognition of unpleasant and pleasant was significantly larger compared to the retrieval of neutral pictures [unpleasant vs. neutral: $F(1, 20) = 13.91, P < 0.001$; pleasant vs. neutral: $F(1, 20) = 8.44, P < 0.001$]. After 1 year, the parietal old/new effect was also significantly more pronounced for unpleasant pictures compared to neutral pictures [$F(1, 20) = 5.48, P < 0.05$]; the old/new difference between pleasant and neutral stimuli, however, was no longer significant [$F(1, 20) < 1$].

Analyzing correctly classified old pictures subdivided into those receiving high- vs. low-confidence responses indicated that this emotional modulation of the parietal ERP old/new effect was exclusively modulated by those correct responses receiving high-confidence ratings [Emo-

tion $\times$ Memory: $F(2, 40) = 5.36, P < 0.05$] and not for those receiving low-confidence ratings [Emotion $\times$ Memory: $F(2, 40) < 1$] again suggesting that the increased parietal ERP old/new deflection for emotional pictures indexes recollection-driven memory retrieval.

sLORETA data: 500–800 ms

The electrical source of activity recorded on the scalp related to episodic memory retrieval was examined with sLORETA for the 500–800 ms time interval. The current source densities displayed one major peak of activity within posterior parietal regions. Analysis of the peak voxels revealed greater parietal voxel activation when old pictures were correctly identified as old, compared to when new pictures were correctly categorized as new [Memory: $F(1, 20) = 17.81, P < 0.001$]. This parietal old/new activation was stronger during retrieval of emotionally arousing stimuli relative to neutral stimuli [Emotion $\times$ Memory: $F(2, 40) = 4.68, P < 0.05, \epsilon = 0.86$; unpleasant vs. neutral: $F(1, 20) = 6.30, P < 0.05$; pleasant vs. neutral: $F(1, 20) = 7.54, P < 0.001$] (see Fig. 3). No effects of time on memory were found by source analyses for the unpleasant, pleasant, and neutral picture category [Emotion $\times$ Memory $\times$ Time: $F(2, 40) = 1.64, P = 0.21$].

Early parietal old/new effect: 300–500 ms

Visual inspection of Figure 1 suggested an early old/new difference in the interval between 300 and 500 ms for unpleasant pictures. Post-hoc analyses indicated an interaction effect of Emotion and Memory [$F(2, 40) = 4.68, P < 0.05, \epsilon = 0.94$] showing that unpleasant pictures elicited a stronger early old/new effect compared to pleasant and neutral pictures [unpleasant vs. neutral: $F(1, 20) = 9.20, P < 0.001$; unpleasant vs. pleasant: $F(1, 20) = 5.44, P < 0.05$]. Moreover, the parietal old/new difference was absent for neutral and pleasant pictures. Time had no effect on this interaction (Emotion $\times$ Memory $\times$ Time, $F < 1$), neither after 1 week nor after 1 year.

DISCUSSION

Emotion, Parietal ERP Old/New Effect, and Memory Recollection

In the current study, we used high-density ERPs to investigate whether long retention intervals can change the neural signature of memory performance during retrieval of emotional and neutral scenes. We provide evidence that enhanced memory for unpleasant and pleasant events compared to neutral events is related to an enhanced parietal ERP old/new effect (500–800 ms) during memory retrieval after 1 week. When measuring ERPs 1 year later, only unpleasant (but not pleasant) pictures showed augmented old/new differences in comparison to the neutral picture category. Analysis of confidence ratings during

Source analysis (sLORETA)

Figure 3.

Source activity associated with correctly judged old and new pictures is plotted for the 1-week condition and each content (pleasant, neutral, and unpleasant), showing the distribution of source activity in the 500–800 ms time interval.

recognition indicate that the memory advantage of emotional relative to neutral stimuli is based on high-confidence responses, suggesting that emotional memory retrieval is driven by the process of recollection.

The results of the present study extend the previous literature reporting long-term memory effects for emotional stimuli [Bradley et al., 1992; Dolcos et al., 2005] by directly examining the neural electrophysiological signature of successful memory retrieval [Rugg and Curran, 2007]. Extending previous ERP findings using shorter retention intervals [Dietrich et al., 2001; Inaba et al., 2005; Koenig and Mecklinger, 2008; Langeslag and van Strien, 2008], we showed enhanced parietal old/new effects for emotional events 1 week (replicating Weymar et al. [2009, 2010]) and 1 year after encoding. This finding gives new support for a memory bias in the ERP old/new effect during long-term retrieval of emotional experiences. Moreover, when subjective confidence ratings during recognition were taken into account, we found that the emotional modulation in behavioral and ERP data was completely driven by high-confidence judgments, indicating that emotion greatly accelerates recognition memory via recollection processes. Recent behavioral evidence using the Remember/Know paradigm [Tulving, 1985] also indicates that emotional pictures were remembered with a greater sense of recollection than neutral pictures [Dolcos et al., 2005; Ochsner, 2000].

The centro-parietal distribution of this old/new effect and the identification of underlying brain sources within the parietal cortex in our data are in agreement with recent functional neuroimaging studies [Vilberg and Rugg, 2009; see for reviews Cabeza et al. [2008] and Wagner et al. [2005]] showing convergent activation for recollection-sensitive old/new effects in the precuneus and the lat-

eral posterior parietal cortex. The results of this research suggest that the parietal fMRI effect and the parietal ERP old/new effect reflect common neural and functional processes [Rugg and Curran, 2007; Vilberg and Rugg, 2009]. Functionally, parietal cortex activation is not essential for successful recollection but may reflect a secondary process integrated within a cortico-hippocampal network that serves an attentional or working memory role [Olson and Berryhill, 2009]. The findings of the current study clearly indicate that parietal lobe contributes to enhanced retrieval of emotionally arousing stimuli. Findings from fMRI support this finding delineating emotional memory networks in frontal cortex, parietal cortex, amygdala, and MTL memory systems during successful retrieval of emotional events [Dolcos et al., 2005; Sterpenich et al., 2009; see for review Buchanan [2007]].

Sustained Long-Term Memory for Unpleasant Pictures

Analyses of behavioral and electrophysiological measures indicate time-specific effects. Memory performance and confidence decreased from 1 week to 1 year. However, superior recognition memory performance for emotional events (unpleasant > pleasant) was stable across both retrieval sessions. In the ERPs, the greater parietal ERP old/new difference for both emotional relative to neutral contents was present during the short delay and persisted for unpleasant memories 1 year after retrieval. Why did unpleasant experiences persist so remarkably well in long-term memory?

From an evolutionary perspective, memory for a dangerous experience should be consistent over time to facilitate avoidance when similar events are re-encountered in the future [Dolan, 2002]. In line, Ochsner [2000] argued that negative material (i.e., human attack, mutilated bodies) may contain more survival-relevant information than positive photographs (pleasant families, cute animals). This distinctiveness of emotional stimuli may enhance memory and preferentially protect unpleasant memory more from forgetting than pleasant memories. Understanding the neural basis of this specific resilience of unpleasant memories to time might even be of clinical value. A recent longitudinal study investigating trauma-related memories by Porter and Peace [2007] reported that traumatic memories are remarkably vivid and persistent even over years, while—at the same time—memories for pleasant events markedly declined. The current findings may suggest that the neural signature is also more persistent for unpleasant memories than for pleasant events.

Because we did not find an interaction effect between Emotion, Memory, and Time in behavior, scalp, and source activity in the current study, a more important factor may be that the long-term negativity bias is caused by the rated arousal level, which is critical for episodic memory [Cahill et al., 1994; LaBar and Cabeza, 2006]. There is increasing evidence that the consolidation of emotional materials underlies noradrenergic transmission in the brain [McGaugh, 2004; Rasch et al., 2009; Weymar et al., 2010]. In the current study sample, arousal ratings were higher for unpleasant than for pleasant pictures, thus may elicit higher noradrenergic activation and subsequent long-term storage. This would strongly conclude that only high arousing memories are resilient to time.

Limitation of the Study and Conclusions

A critical limitation of the study is that the present results do not address the issue of sex differences in emotional memory. Previous evidence indicates that different neural circuits are involved in men and women when activating their emotional long-term episodic and autobiographical memory [Cahill, 2006; Canli et al., 2002; Piefke et al., 2005; Wang et al., 2010]. Because we only used male participants, we cannot rule out that the emotional ERP old/new effects obtained for the two test delays are different for men and women. Future research should investigate whether the emotional modulation of the long-term old/new effect is modulated by gender.

Taken together, the present study investigated electrical brain responses during long-term recollection of emotional and neutral pictures after two retention delays (1-week vs. 1-year). Our results indicate that the retrieval of emotional pictures is associated with an enhanced ERP old/new effect over parietal regions, reflecting conscious recollection for this material. We provided evidence that enhanced memory for unpleasant and pleasant pictures compared to

neutral pictures is reflected by a larger parietal ERP old/new effect after a 1-week delay. Moreover, when remembering emotional pictures after a 1-year delay, only unpleasant (but not pleasant) showed augmented old/new differences relative to the neutral picture category, suggesting that the memory trace for unpleasant (high arousing) experiences is remarkable strong and long-lasting.

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REFERENCES

- Anderson AK, Yamaguchi Y, Grabski W, Lacka D (2006): Emotional memories are not all created equal: Evidence for selective memory enhancement. *Learn Mem* 13:711–718.
- Bradley MM, Lang PJ (1994): Measuring emotion: The self-assessment manikin and the semantic differential. *J Behav Ther Exp Psychiatry* 25:49–59.
- Bradley MM, Greenwald MK, Petry MC, Lang PJ (1992): Remembering pictures: Pleasure and arousal in memory. *J Exp Psychol Learn Mem Cogn* 18:379–390.
- Buchanan TW (2007): Retrieval of emotional memories. *Psychol Bull* 133:761–779.
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M (2008): The parietal cortex and episodic memory: An attentional account. *Nat Rev Neurosci* 9:613–625.
- Cahill L (2006): Why sex matters for neuroscience. *Nat Rev Neurosci* 7:477–484.
- Cahill L, Prins B, Weber M, McGaugh JL (1994): Beta-adrenergic activation and memory for emotional events. *Nature* 371:702–704.
- Canli T, Desmond JE, Zhao Z, Gabrieli JDE (2002): Sex differences in the neural encoding of emotional experiences. *Proc Natl Acad Sci USA* 99:10789–10794.
- Curran T, Cleary AM (2003): Using ERPs to dissociate recollection from familiarity in picture recognition. *Brain Res Cogn Brain Res* 15:191–205.
- Curran T, Friedman WJ (2004): ERP old/new effects at different retention intervals in recency discrimination tasks. *Brain Res Cogn Brain Res* 18:107–120.
- Dietrich DE, Waller C, Johannes S, Wieringa B, Emrich HM, Münte TF (2001): Differential effects of emotional content on event-related potentials in word recognition memory. *Neuropsychobiology* 43:96–101.
- Dolan RJ (2002): Emotion, cognition, and behavior. *Science* 298:1191–1194.
- Dolcos F, LaBar KS, Cabeza R (2005): Remembering one year later: Role of the amygdala and medial temporal lobe memory system in retrieving emotional memories. *Proc Natl Acad Sci USA* 102:2626–2631.
- Duarte A, Ranganath C, Winward L, Hayward D, Knight RT (2004): Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. *Brain Res Cogn Brain Res* 18:255–272.
- Düzel E, Yonelinas AP, Mangun GR, Heinze H-J, Tulving E (1997): Event-related brain potential correlates of two states of

- conscious awareness in memory. *Proc Natl Acad Sci USA* 94:5973–5978.
- Düzel E, Vargha-Khadem F, Heinze HJ, Mishkin M (2001): Brain activity evidence for recognition without recollection after early hippocampal damage. *Proc Natl Acad Sci USA* 98:8101–8106.
- Friedman D, Johnson RJ (2000): Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microsc Res Tech* 51:6–28.
- Inaba M, Nomura M, Ohira H (2005): Neural evidence of effects of emotional valence on word recognition. *Int J Psychophysiol* 57:165–173.
- Johansson M, Mecklinger A, Treese AC (2004): Recognition memory for emotional and neutral faces: An event-related potential study. *J Cogn Neurosci* 16:1840–1853.
- Junghöfer M, Peyk P (2004): Analysis of electrical potentials and magnetic fields of the brain. *Matlab Select* 2:24–28. EMEGS software is freely available at <http://www.emegs.org>.
- Junghöfer M, Elbert T, Tucker D, Rockstroh B (2000): Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology* 37:523–532.
- Koenig S, Mecklinger A (2008): Electrophysiological correlates of encoding and retrieving emotional events. *Emotion* 8:162–173.
- LaBar KS, Cabeza R (2006): Cognitive neuroscience of emotional memory. *Nat Rev Neurosci* 7:54–64.
- Lang PJ, Bradley MM, Cuthbert BN (2008): International Affective Picture System (IAPS): Affective Ratings of Pictures and Instruction Manual. Technical Report A-8. Gainesville, FL: University of Florida.
- Langeslag SJ, van Strien JW (2008): Age differences in the emotional modulation of ERP old/new effects. *Int J Psychophysiol* 70:105–114.
- McGaugh JL (2004): The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annu Rev Neurosci* 27:1–28.
- Ochsner KN (2000): Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *J Exp Psychol Gen* 129:242–261.
- Olson IR, Berryhill ME (2009): Some surprising findings on the involvement of the parietal lobe in human memory. *Neurobiol Learn Mem* 91:155–165.
- Pascual-Marqui RD (2002): Standardized low resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods Find Exp Clin Pharmacol* 24 Suppl D:5–12.
- Piefke M, Weiss PH, Markowitsch HJ, Fink GR (2005): Gender differences in the functional neuroanatomy of emotional episodic autobiographical memory. *Hum Brain Mapp* 24:313–324.
- Porter S, Peace K (2007): The scars of memory: A prospective, longitudinal investigation of the consistency of traumatic and positive emotional memories in adulthood. *Psychol Sci* 18:435–441.
- Rasch B, Spalek K, Buholzer S, Luechinger R, Boesiger P, Papassotiropoulos A, de Quervain DJF (2009): A genetic variation of the noradrenergic system is related to differential amygdala activation during encoding of emotional memories. *Proc Natl Acad Sci USA* 106:19191–19196.
- Ritchey M, Dolcos F, Cabeza R (2008): Role of amygdala connectivity in the persistence of emotional memories over time: An event-related fMRI investigation. *Cereb Cortex* 18:2494–2504.
- Rugg MD, Curran T (2007): Event-related potentials and recognition memory. *Trends Cogn Sci* 11:251–257.
- Schupp HT, Junghöfer M, Weike AI, Hamm AO (2003): Emotional facilitation of sensory processing in the visual cortex. *Psychol Sci* 14:7–13.
- Schupp HT, Stockburger J, Codispoti M, Junghöfer M, Weike AI, Hamm AO (2007): Selective visual attention to emotion. *J Neurosci* 27:1082–1089.
- Stark R, Schienle C, Girod C, Walter B, Kirsch P, Blecker C et al. (2005): Erotic and disgust-inducing pictures: Differences in the hemodynamic responses of the brain. *Biol Psychol* 70:19–29.
- Sterpenich V, Albouy G, Darsaud A, Schmidt C, Vandewalle G, Dang Vu TT, Desseilles M, Phillips C, Degueldre C, Baletau E, Collette F, Luxen A, Maquet P (2009): Sleep promotes the neural reorganization of remote emotional memory. *J Neurosci* 29:5143–5152.
- Tulving E (1985): Memory and consciousness. *Can Psychol* 26:1–12.
- Vilberg KL, Rugg MD (2009): Functional significance of retrieval-related activity in lateral parietal cortex: Evidence from fMRI and ERPs. *Hum Brain Mapp* 30:1490–1501.
- Voss JL, Paller KA (2008): Brain substrates of implicit and explicit memory: The importance of concurrently acquired neural signals of both memory types. *Neuropsychologia* 46:3021–3029.
- Wagner A, Shannon B, Kahn I, Buckner R (2005): Parietal lobe contributions to episodic memory retrieval. *Trends Cogn Sci* 9:445–453.
- Wang HB, Ma N, Yu YQ, Chen YR, Wank K, Zhang DR (2010): Is the contribution of the amygdala to the sex- and enhancement-related effects of emotional memory time-dependent? *Neurobiol Learn Mem* 93:1–7.
- Weymar M, Löw A, Melzig CA, Hamm AO (2009): Enhanced long-term recollection for emotional pictures: Evidence from high-density ERPs. *Psychophysiology* 46:1200–1207.
- Weymar M, Löw A, Modess C, Engel G, Gründling M, Petersmann A, Siegmund W, Hamm AO (2010): Propranolol selectively blocks the enhanced parietal old/new effect during long-term recollection of unpleasant pictures: A high density ERP study. *Neuroimage* 49:2800–2806.
- Wixted JT, Stretch V (2004): In defense of the signal detection interpretation of remember/know judgements. *Psychon Bull Rev* 11:616–641.
- Wolk DA, Schacter DL, Lygizos M, Sen NM, Holcomb PJ, Daffner KR, Budson AE (2006): ERP correlates of recognition memory: Effects of retention interval and false alarms. *Brain Res* 1096:148–62.
- Yonelinas AP (2001): Consciousness, control, and confidence: The 3 Cs of recognition memory. *J Exp Psychol* 130:361–379.
- Yonelinas AP (2002): The nature of recollection and familiarity: A review of 30 years of research. *J Mem Lang* 46:441–517.