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Encoding-related EEG oscillations during memory formation are modulated by mood state

Matti Gärtner[1,2] **and Malek Bajbouj**[1,2]

[1]Cluster of Excellence "Languages of Emotion", Freie Universität Berlin, 14195 Berlin, Germany and [2]Department of Psychiatry, Charité University Medicine Berlin, Campus Benjamin Franklin, 14050 Berlin, Germany

Mood states have a strong impact on how we process incoming information. It has been proposed that positive mood facilitates elaborative, relational encoding, whereas negative mood promotes a more careful, stimulus-driven encoding style. Previous electrophysiological studies have linked successful information encoding to power increases in slow (<8 Hz) delta/theta and fast (>30 Hz) gamma oscillations, as well as to power decreases in midrange (8–30 Hz) alpha/beta oscillations. Whether different mood states modulate encoding-related oscillations has not been investigated yet. In order to address this question, we used an experimental mood induction procedure and recorded electroencephalograms from 20 healthy participants while they performed a free recall memory task after positive and negative mood induction. We found distinct oscillatory patterns in positive and negative mood. Successful encoding in positive mood was accompanied by widespread power increases in the delta band, whereas encoding success in negative mood was specifically accompanied by frontal power decreases in the beta band. On the behavioral level, memory performance was enhanced in positive mood. Our findings show that mood differentially modulates the neural correlates of successful information encoding and thus contribute to an understanding of how mood shapes different processing styles.

Keywords: subsequent memory paradigm; mood induction; EEG; delta ERS; beta ERD

INTRODUCTION

Over the last two decades the interdependence of cognition and emotion has become a major research interest in cognitive neuroscience (Damasio 1994; Ledoux 1996; Dolan 2002; Pessoa 2008). So far, the focus of many studies has been to investigate how emotionally valenced material affects different cognitive processes such as attention (e.g. Vuilleumier 2005), or memory (e.g. LaBar and Cabeza 2006). Another interesting question that has been addressed less frequently is how longer-lasting emotional states such as mood affect cognitive processing independent of stimulus valence.

In the field of behavioral psychology, numerous studies have demonstrated that information is processed differently in positive and negative mood states (for review, see Clore and Huntsinger 2007). A possible explanation for these differences is provided by the affect-as-information hypothesis (Schwarz and Clore 1983). According to this hypothesis, affective states such as mood inform an individual about the nature of the current situation. Whereas a negative mood state signals a problematic situation where negative outcomes pose a potential threat, a positive mood state informs the individual that the current situation is unproblematic and negative outcomes do not pose any threats. The hypothesis further proposes that this mood-based evaluation of the situation leads to different processing strategies during cognitive tasks. In positive mood, simple heuristics might be preferred to more effortful, detail-oriented strategies. Furthermore, unusual creative associations may be elaborated. In contrast, negative mood leads to a careful, systematic, bottom-up processing style to avoid negative outcome. In line with these assumptions empirical research has shown that positive mood states lead to global, category-level, relational processing, whereas negative mood states lead to local, item-level, stimulus-specific processing (Ashby *et al.*, 1999; Fiedler 2001; Martin and Clore 2001).

Studies investigating the effects of mood on memory performance report a variety of results depending on the utilized memory task. In line with the afore-mentioned theoretical assumptions, it has been demonstrated that people in positive mood show enhanced memory performance (Isen *et al.*, 1978; Nasby and Yando 1982; Fiedler *et al.*, 2003), especially in tasks requiring elaboration (Leight and Ellis 1981; Ellis *et al.*, 1984; Kensinger *et al.*, 2002; Erk *et al.*, 2003). These findings are supported by the levels of processing framework that proposes a link between depth of processing and memory performance (Craik and Lockhart 1972). A deeper, elaborative processing style leads to enhanced recall rates, e.g. by providing additional retrieval paths (Craik and Tulving 1975). On the contrary, it has also been found that people in negative mood show enhanced performance in tasks that require accurate stimulus perception (Fiedler *et al.*, 2003; Storbeck and Clore 2005). It is important to note that two basic phenomena have to be considered when studying mood effects on memory performance: state dependence and mood congruence (Blaney 1986). Whereas the first one describes effects of the mood state that are independent of stimulus material, the latter describes the effect of superior recall when the mood state at encoding or retrieval matches the valence of emotional stimulus material (Bower 1981). A prerequisite to measure pure state effects is neutral stimulus material.

The above-mentioned behavioral evidence suggests that information encoding in positive and negative mood states is based on different neural processes. In brain imaging and electrophysiological studies, the neural mechanisms during episodic encoding are often studied in a subsequent memory paradigm (Paller and Wagner 2002). Neural activity for later remembered (LR) items is compared with neural activity for later forgotten (LF) items. Differential activations (LR − LF) are called subsequent memory effect (SME). Some studies investigated the SME in different mood conditions (Kiefer *et al.*, 2007; Fitzgerald *et al.*, 2011). However, these studies focused on mood congruency effects, and therefore applied emotional stimulus material. In one functional MRI (fMRI) study, neutral material was applied to investigate the SME

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Correspondence should be addressed to Matti Gärtner, Cluster "Languages of Emotion", Freie Universität Berlin, Habelschwerdter Allee 45, 14195 Berlin, Germany. E-mail: matti.gaertner@fu-berlin.de

in different emotional contexts (Erk *et al.*, 2003). The emotional context consisted of emotional pictures that preceded each of the to-be-remembered items. In this study it was demonstrated that in a positive emotional context LR words elicit more activity in the right parahippocampal and fusiform gyrus, whereas in a negative context activity was greater in the amygdalar region. However, what remains unclear is whether the emotional context induced different mood states (Lewis and Critchley 2003; Walter *et al.*, 2003).

Independent of an experimental mood manipulation, event-related changes in neural oscillations have been linked to encoding processes during memory formation in several electrophysiological studies (for review, see Nyhus and Curran 2010). These oscillatory SMEs have been linked to both, processes of neural synchronization and processes of neural desynchronization.

Event-related synchronization (ERS) during encoding has been observed in the delta (1–4 Hz) and theta (4–8 Hz) band (Klimesch *et al.*, 1996; Weiss and Rappelsberger 2000; Sederberg *et al.*, 2003; Summerfield and Mangels 2005; Osipova 2006). Furthermore, ERS in the gamma band (30–100 Hz) has been linked to encoding (Sederberg *et al.*, 2003; Osipova 2006; Sederberg *et al.*, 2007). Although theta SMEs have mainly been reported in frontal and temporal regions (Klimesch *et al.*, 1999; Sederberg *et al.*, 2003; Hanslmayr *et al.*, 2009), delta and gamma SMEs have been reported in widespread electrode locations (Sederberg *et al.*, 2003; Serruya *et al.*, 2014). The functional role of neural synchronization as a general mechanism of information processing has been intensively discussed during the last decade (Engel *et al.*, 2001; Varela *et al.*, 2001; Buzsaki and Draguhn 2004). A general consensus is that communication between distributed neural sources is facilitated by synchronized neural activity (Siegel *et al.*, 2012). With respect to encoding processes during memory formation it has been proposed that neural synchronization allows for the transient interaction between cortical structures and the hippocampus (Nyhus and Curran 2010) and shapes synaptic plasticity (Axmacher *et al.*, 2006; Fell and Axmacher 2011).

Event-related desynchronization (ERD) during memory formation has been observed in the alpha (8–13 Hz) and beta (15–30 Hz) band (Klimesch *et al.*, 1997; Hanslmayr *et al.*, 2009, 2011; Meeuwissen *et al.*, 2011). Processes of neural desynchronization have been linked to the activation of local cortical structures in simultaneous electroencephalogram (EEG)–fMRI experiments (Ritter *et al.*, 2009; Scheeringa *et al.*, 2011). During memory formation, SMEs in the alpha band have been linked to attentional and semantic processing (Klimesch *et al.*, 1999), whereas beta SMEs have specifically linked to semantic processing (Hanslmayr *et al.*, 2009). Using a subsequent memory paradigm, Hanslmayr *et al.*, (2011) showed that ERD in the beta band correlated positively with activity in the inferior frontal gyrus (IFG) an area that has been tightly linked to semantic processing in several fMRI studies (Kim 2011). Using source localization, Meeuwissen *et al.*, (2011) also found a beta SME in left-frontal sensor locations that was localized in the IFG.

Given these findings, the aim of this study was to investigate whether different mood states selectively modulate performance and encoding-related oscillatory EEG patterns in a memory task that requires elaborative, relational processing (free recall of word lists). We applied a 2 × 2 within subjects design with memory (LR *vs* LF) and mood (positive mood *vs* negative mood) as factors. We hypothesized performance benefits in positive mood because our task required elaborative processing. Regarding the oscillatory SMEs, we hypothesized ERD in the alpha and beta band because our task strongly depended on semantic processing. Especially, we hypothesized strong ERD effects in the beta band in frontal sensors, because this SME has been linked to deep semantic processing. Furthermore, we hypothesized ERS in slow (delta/theta) and fast (gamma) frequency ranges that have been related to memory formation. As our memory task was intentional, these SMEs that are directly involved in the formation of long-term memories can be expected. In line with previous research, we hypothesized theta SMEs to be located in frontal sensors and delta and gamma SMEs in widespread sensor locations. Expectations about mood-dependent modulations of these SMEs were formulated according to the following rationale: positive mood facilitates a processing style that is based on the integration of new information into preexisting knowledge structures. It can be expected that this type of processing involves the coordination of multiple neural sources. Therefore, encoding-related neural synchronization might be enhanced during positive mood. In contrast, negative mood facilitates a processing style that is focused on accurate stimulus perception and item-level encoding. This type of processing might facilitate the activation of local brain regions involved in semantic processing and therefore might be accompanied by enhanced encoding-related neural desynchronization.

METHODS

Participants

Twenty healthy, right-handed participants (13 females, ages: 24–35 years) participated in the study. Participants were selected from a large database available to our research group. In a previous study, they were screened for verbal intelligence (Mehrfachwahl Wortschatz Intelligenztest, MWT-A; Lehrl et al. 1995) and response to emotional stimuli (rating of pictures from the international affective picture system, IAPS; Lang et al. 2008). Verbal intelligence scores below average and no response to emotional stimuli served as exclusion criteria. All participants signed a written consent after the experiment had been explained to them. They were paid 30 Euro for their participation. The local ethics committee of the Charité approved the study.

Material and procedure

Upon arrival participants were instructed about the nature and the procedure of the experiment. They were seated in front of a computer screen where the experiment and the preparation of the EEG cap took place. During EEG preparation they received further instructions and were introduced to different elaborative mnemonics, such as the 'method of loci' (Bower 1970) and other related methods. Before the experiment started participants practiced the relatively demanding free recall task for several rounds. Afterwards, the light in the room was dimmed to increase the cinematic effect of the film clips and the experiment started.

In total, the experiment consisted of 12 blocks. Each block started with a short (3–5 min) film clip (see below) with either pleasant or unpleasant content to induce a positive or a negative mood state, respectively. In order to increase the effect of the mood induction, two successive blocks contained two clips of the same emotional category. Across participants the clips were shown in one of two possible orders. The experiment started either with two pleasant clips or with two unpleasant clips. The order of the clips is shown in Table 1. In each block, the film clip was followed by a 1 min eyes-closed resting period in which participants were asked to contemplate on the content of the clip. Thereafter participants had to rate whether the last clip had an effect on their current mood state (9-point rating scale, range: −4 to 4). Participants were instructed to select negative rating values when they observed a negative influence of the last clip on their current mood state. Positive rating values were selected if a positive influence on the mood state was observed. If participants felt that their mood state had not been affected at all, they selected the '0' in the middle of the rating scale. After the rating the main task followed.

A sequence of 20 neutral nouns was presented at a 2.75 s rate. Words stayed on the screen for 1000 ms and were separated by an

Table 1 Description of all film clips used during the experiment

Order	Film	Clip	Origin	Seconds	Mood
1 (11)	Baraka	Documentary about chicken factory farming	Private	125	Negative
2 (12)	Sleepers	Sexual abuse of children in a prison	Filmstim	140	Negative
3 (1)	Deep Blue	Dolphins swim through the waves	Private	130	Positive
4 (2)	Mr Bean	Mr Bean moves his furniture in his car	Private	163	Positive
5 (3)	Amistad	Slaves are thrown overboard of a slave ship	Private	119	Negative
6 (4)	Saving Private Ryan	War scene: fighting on the beaches	Filmstim	196	Negative
7 (5)	Benny and Joon	Johnny Depp plays the fool in a coffee shop	Filmstim	121	Positive
8 (6)	Ghost	Love/dance scene with a couple	Filmstim	215	Positive
9 (7)	The Cove	Dolphin hunters killing dozens of dolphins	Private	200	Negative
10 (8)	Schindler's List	Dead bodies in a concentration camp scene	Filmstim	78	Negative
11 (9)	The Dead Poets Society	Students climb on their desks for their teacher	Filmstim	160	Positive
12 (10)	BBC—Planet Earth	A polar bear mother with her two babies	Private	167	Positive

In the first column, the numbers in brackets depict the order that one-half of the subjects received for counterbalancing reasons.

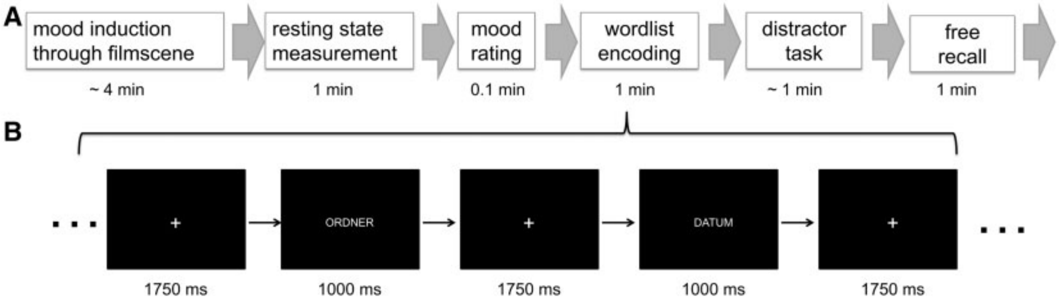

Fig. 1 Experimental design. Timeline of one experimental block (A) and screenshots of an example sequence of the wordlist encoding task (B).

interstimulus interval of 1750 ms during which a fixation cross was presented (Figure 1). The width of the word stimuli varied between 3 and 6.5 cm depending on the word length (visual angle: 2.3°–4.9°). All nouns were selected from the Berlin Affective Word List (Vo *et al.*, 2009) and were matched condition- and blockwise for their length, imageability and frequency, as well as for their valence and arousal. Additionally, word sequences were counterbalanced across participants, such that all words appeared equally often in positive and negative mood blocks. For each word sequence, participants were instructed to try to remember as many words as possible. They were encouraged to make use of elaborative mnemonics that had been presented to them in the preparation phase.

Each word sequence was followed by a distractor task in which participants had to solve four moderately difficult arithmetic operations for approximately 1 min. In the final part of each block, participants underwent a 1 min free recall period in which they had to orally enumerate all words they could remember from the last sequence. During that period, a voice recording was automatically activated. After a short break the next block started with the next film clip. The timeline of one experimental block is shown in Figure 1. The total duration of the experiment was approximately 1.5 h.

Film clips

A total of 12 film clips were shown during the experiment. The clips were selected from international movies (German versions). Half of the clips were selected from a large database of emotion eliciting films (Schaefer *et al.*, 2010) that is freely available on the internet. The other half of the clips was selected from a private film collection. The effectiveness of the film clips in terms of inducing a positive or a negative mood state was tested in an independent sample of 10 participants prior to the experiment. An overview of all clips is given in Table 1.

EEG recording and data analyses

EEG data were recorded from 61 Ag/AgCl scalp electrodes (BrainCap64, Easycap, Herrsching-Breitbrunn, Germany), arranged according to the extended 10–20 system. Vertical eye movements and blinks were additionally recorded from an electrode placed below the right eye. Furthermore, we recorded heart rate data from two bipolar electrodes on the upper part of the chest. An electrode placed on the nose tip served as common reference for all channels. Signals were amplified using an analog 0.1 Hz highpass—and a 1000 Hz lowpass filter. Internally, signals were digitized with a sampling rate of 5000 Hz. Before signals were saved to disk with a sampling rate of 1000 Hz a digital 450 Hz anti-aliasing filter was applied (BrainAmpMR plus, Brain Products, Gilching, Germany). All further data- and statistical analysis was carried out in Matlab (Version R2010b, The MathWorks, Inc., MA, USA), using custom scripts as well as the EEGLAB (Delorme and Makeig 2004) and Fieldtrip (Oostenveld *et al.*, 2011) toolboxes.

For analyses, EEG data of the encoding phase of the memory task were used (12 block ~ 12 min). Data were resampled to 200 Hz, re-referenced to a common average reference and 1 Hz highpass filtered. Next, slightly overlapping epochs (−1 to 2 s relative to word onsets) were extracted. Artifact removal from the epoched data sets proceeded as follows: First, epochs that were contaminated with motion-related artifacts or exceeded a threshold of ±100 μV were removed using semiautomatic rejection methods available in the EEGLAB toolbox. Next, an infomax independent component analysis (ICA)(Bell and Sejnowski 1995) was applied to the cleaned data sets. Eye

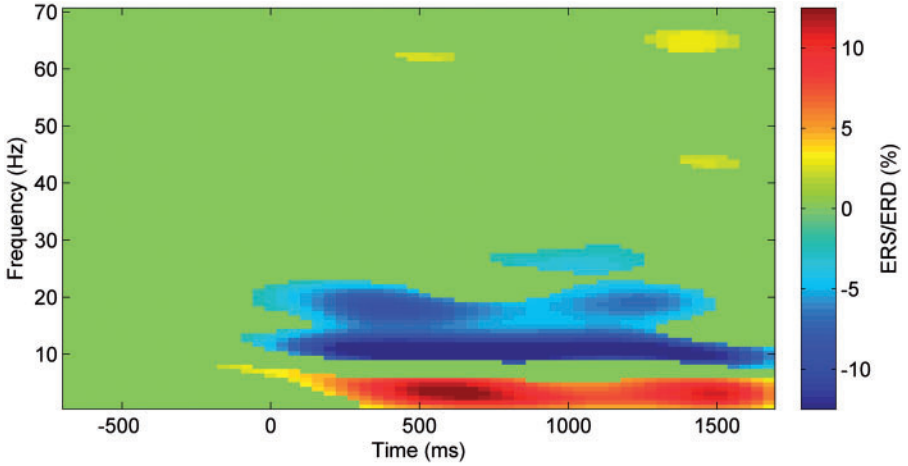

Fig. 2 Time–frequency ranges involved in encoding. Effects of ERS and ERD are shown as percent changes from a prestimulus baseline period (−1000 to 0 ms). Only significant regions with a percent change >2% are shown (alpha = 0.05, FDR corrected). The time of the stimulus onset was at 0 ms.

movement-related components were identified by visual inspection and removed from the data. Stimulus-evoked (phase-locked) responses were removed from the data by subtracting for each condition the average waveform from the waveform of each individual trial.

Time–frequency analysis was carried out using the *newtimef* function from the EEGLAB toolbox. A Hanning tapered zero-padded fast Fourier transform (FFT) was applied to estimate spectral power at 128 linear spaced frequencies (1–100 Hz). The window size of the moving FFT window was set to 640 ms. The step size was set to 40 ms resulting in 60 time points. Event-related power changes were calculated as the percentage change of power in relation to a prestimulus (−1000 to 0 ms) baseline (Pfurtscheller and Aranibar 1977). Time–frequency representations of each subject were convolved with a 3 Hz × 300 ms (full width at half maximum, FWHM) Gaussian kernel.

In the first step of our statistical analysis, we identified the frequency ranges involved in encoding. We conducted a one-sample *t*-test pooled across all conditions and channels. The false discovery rate (FDR) algorithm was used to correct for multiple comparisons (Benjamini and Hochberg 1995). Furthermore, observed percent changes below 2% were discarded. In the next step, we tested whether the observed frequency ranges differed between LR and LF items. For this analysis, we used a cluster-based permutation approach to account for multiple testing (Maris and Oostenveld 2007). For each subject and condition, we calculated a three-dimensional statistical parametric map (*t*-test, alpha = 0.05) in the sensor–time–frequency space (for details of the procedure, see e.g. Kilner *et al.*, 2005). A cluster was defined as the sum of *t*-values in adjacent sensor–time–frequency bins. Adjacency in the sensor space was taken as a given if at least two neighboring sensors belonged to a cluster. The alpha level for the cluster analysis was set to 0.05 (corrected) and the number of random permutations was set to 1000. In the next step, we tested whether the observed clusters were modulated by mood state. We repeated the above-described cluster analysis for separate mood conditions. Furthermore, we tested the interaction with the mood factor directly by conducting a further subsequent cluster analysis in which we contrasted the differences (LR positive mood − LF positive mood) and (LR negative mood − LF negative mood).

RESULTS

Behavioral results

Mood ratings after positive film clips (mean: 1.41; s.d.: 0.86) were higher than mood ratings after negative film clips (mean: −1.50; s.d.: 0.84; *t*-test, $P < 0.0001$). Memory performance (number of correctly remembered words) was enhanced in positive mood (mean: 9.37; s.d.: 2.86) compared with negative mood (mean: 8.49; s.d.: 2.68; *t*-test, $P < 0.001$). Correlation analysis between subjective mood ratings and memory performance revealed a linear relationship between mood and memory (Pearson correlation, $r = 0.66$, $P < 0.05$). All participants reported to have used the suggested elaborative mnemonics to study the wordlists. An additional control analysis showed that the order of the mood induction did not influence the mood-dependent memory performance [analysis of variance, ANOVA, $f(1,18) = 0.99$, $P = 0.33$].

EEG results

The most prominent encoding-related oscillatory changes were observed in two frequency ranges (Figure 2). ERS was mainly observed in the delta/theta frequency range (1–8 Hz), and ERD was observed in the alpha/beta range (8–30 Hz). Frequency ranges above 30 Hz revealed only minor encoding-related changes in the gamma band (~60 Hz).

Cluster analysis in the observed encoding-related frequency ranges revealed one significant SME in the delta/theta (2–8 Hz) band (cluster statistic, $P = 0.039$) in a time range from 0 to 760 ms. ERS in this cluster was stronger for LR items than for LF items (ERS cluster) and it was located in left-frontal, frontal-midline and right-parietal sensors. A second SME was observed in the beta (16–29 Hz) band (cluster statistic, $P = 0.012$) in a time range from 360 to 1480 ms. ERD in this cluster was stronger for LR items than for LF items (ERD cluster) and it was located in left-parietal sensors. The observed encoding-related changes in the alpha and gamma band did not show any significant SMEs. Statistical parameters and dimensions of two observed SME clusters are given in Table 2 and Figure 3.

Based on these findings, subsequent cluster analysis for separate mood conditions revealed one highly significant ERS cluster (cluster statistic, $P = 0.006$) in positive mood in the delta/slow theta range (2–5 Hz) that was present in widely distributed sensor location with a right-frontal/left-parietal focus. In negative mood, no significant clusters were observed in the delta/theta range. However, one ERS cluster in the theta (4–8 Hz) range in negative mood showed a trend (cluster statistic, $P = 0.096$). This cluster was mainly observed in left-frontal sensors. Direct comparison of the SMEs in positive and negative mood in the delta/theta frequency range revealed that successful encoding in positive mood was specifically reflected by ERS in the delta range (2–4 Hz) in left-parietal sensors (cluster statistic, $P = 0.035$).

For visualization see Figure 4 and Table 2 for statistics and cluster dimensions.

In negative mood, a highly significant ERD cluster (cluster statistic, $P = 0.003$) was observed in the beta band (17–27 Hz) which was located in left-frontal and left-parietal sensors. In positive mood, none of the observed ERD clusters reached significance. However, one ERD cluster in positive mood showed a trend (cluster statistic, $P = 0.093$) in a narrow beta frequency range (22–27 Hz) which was located in left-parietal sensors. Direct comparison of the SMEs in positive and negative mood revealed that encoding success in negative mood was specifically reflected by ERD in the beta range (19–26 Hz) in frontal sensors (cluster statistic, $P = 0.047$). Visualization, statistics and cluster dimensions are given in Figure 5 and Table 2.

DISCUSSION

In this study, we investigated the effects of mood on memory performance and on encoding-related processes in oscillatory EEG activity. To assure that the observed effects are purely state dependent, we utilized neutral stimulus material that was carefully matched across mood conditions. As predicted, we found that a positive mood state leads to enhanced recall rates. Most likely this effect depends on the relatively demanding free recall memory paradigm we utilized. Such a memory paradigm requires elaborative processing, which has been shown to be facilitated in positive mood (Fiedler 2001; Forgas 2001; Clore and Huntsinger 2007). This explanation is further supported by the fact that all participants reported to have used elaborative encoding strategies during the experiment.

In the EEG, two oscillatory SMEs were observed. In line with previous research, successful memory formation was predicted by stronger ERS in the delta/theta frequency range (2–8 Hz) and by stronger ERD in the beta range (16–29 Hz). Remarkably, both observed SMEs were profoundly modulated by mood state. As predicted, successful memory formation in positive mood was predominately accompanied by a process of neural synchronization, whereas memory formation in negative mood was predominately accompanied by a process of neural desynchronization.

Processes of neural synchronization during memory formation have been linked to the temporal integration of input from distributed cortical areas (Nyhus and Curran 2010). We hypothesized that elaborative, relational processing which is facilitated in positive mood might predominantly rely on such a synchronization mechanism. During elaborative, relational processing incoming information is being related to preexisting knowledge structures. The activation of these structures could be realized by processes of neural synchronization. Our results strongly support this idea for several reasons. In positive mood we observed a highly significant ERS cluster, whereas such a cluster was absent in negative mood. Furthermore, the direct comparison between the SMEs in positive and negative mood revealed that successful memory formation in positive mood was specifically related to an ERS mechanism. The widely distributed sensor locations in positive mood also point to an enhancement of relational processing in positive mood. An interesting finding is that the relatively broad frequency range of ERS effect for pooled mood conditions (2–8 Hz) was split into two distinct frequency ranges in positive (2–4 Hz) and

Table 2 Cluster statistics and dimensions

Condition	Cluster size (*t*-sum)	*P*-value	Frequency range (Hz)	Time window (ms)	Location
ERS clusters					
Pooled	2020	0.039*	1.6–7.8	0–760	LF MF RP
Positive	2012	0.006**	1.6–4.7	0–680	MF RF LP
Negative	531	0.096^{+}	3.9–7.8	0–480	LF MF
Interaction	1166	0.035*	1.6–3.9	0–640	LP MP
ERD clusters					
Pooled	5168	0.012*	16.4–28.9	360–1480	LP MP
Positive	741	0.093^{+}	21.9–27.3	880–1480	LP
Negative	4447	0.003**	17.2–27.3	440–1280	LF MF LP
Interaction	1343	0.047*	19.5–25.8	600–1200	LF MF RF

Cluster size values are based on the sum of all *t*-values in the observed clusters. *P*-values are determined by the number of random permutation clusters that showed a larger cluster sizes than the observed clusters. LF, left-frontal; FM, frontal-midline; RF, right-frontal; LP, left-parietal; PM, parietal-midline; RP, right-parietal.**, $p < 0.01$; *, $p < 0.05$; $^{+}$, $p < 0.1$.

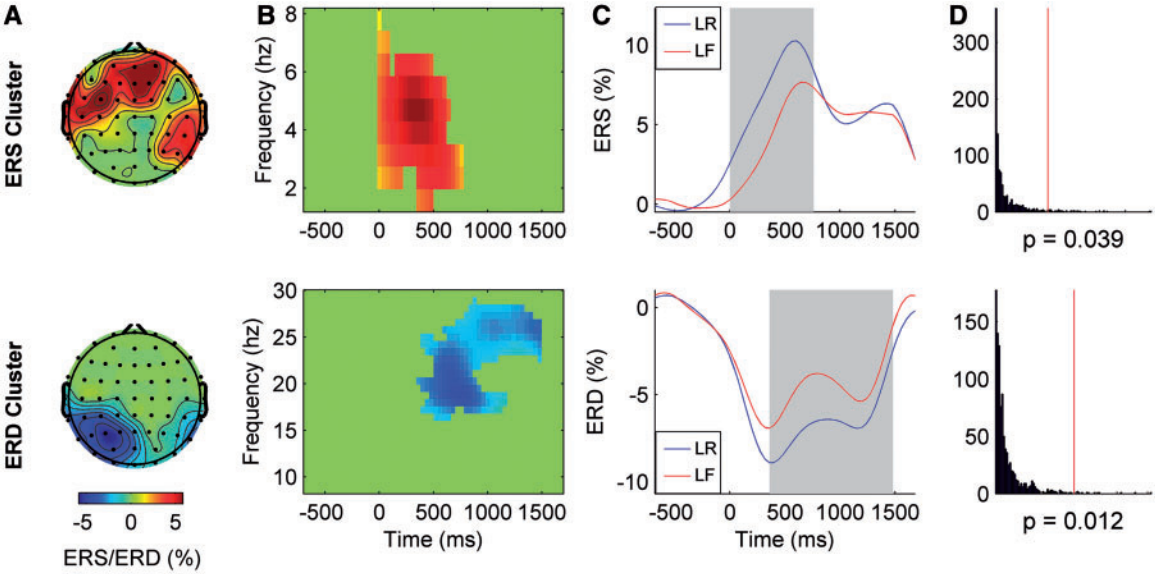

Fig. 3 SMEs for pooled mood conditions. Visualization of the ERS and the ERD cluster in the sensor–time–frequency space. Cluster dimensions in the (A) sensor space and (B) time–frequency space. (C) Averaged cluster time courses for LR and LF items. (D) Distribution of random clusters in the cluster-based permutation test. The red line marks the position of the observed cluster. All ERS/ERD values depict percent changes from a prestimulus baseline period (−1000 to 0 ms). In (A) and (B), difference values (LR − LF) are shown. In (C), percent changes for LR and LF items are shown as separate lines. The time of the stimulus onset was at 0 ms [(B) and (C)].

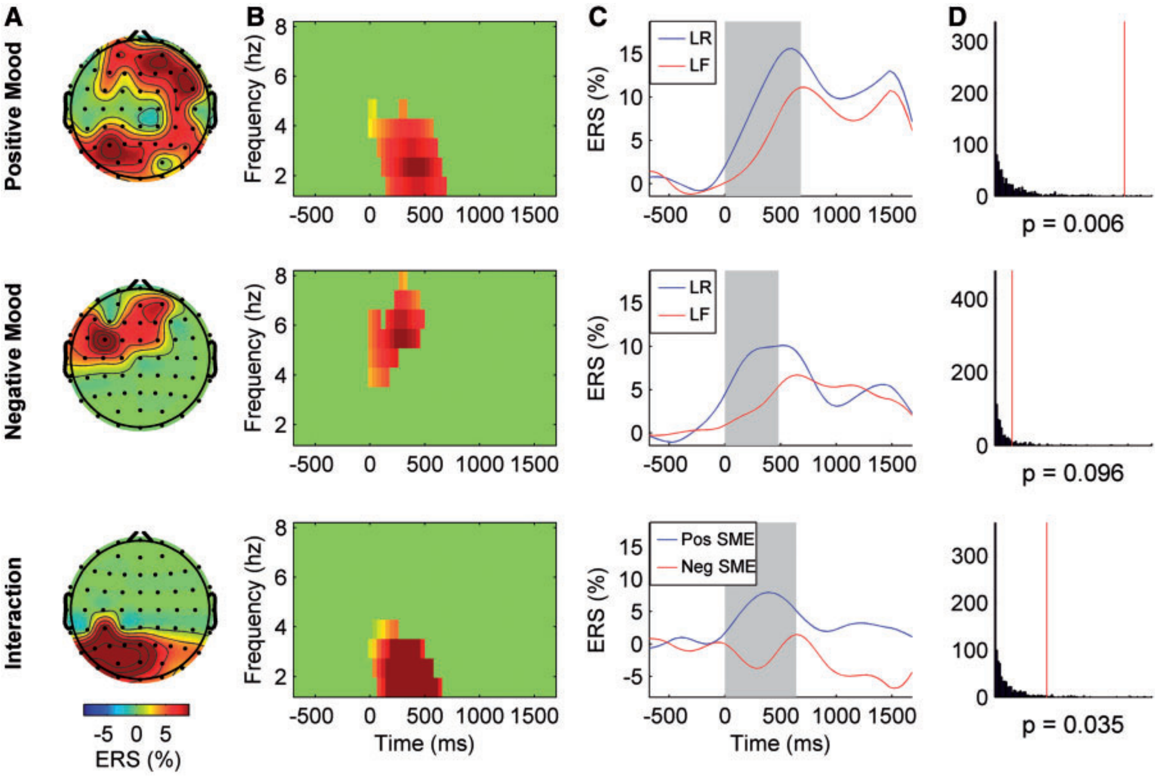

Fig. 4 Effects of mood on ERS SMEs. ERS clusters in the sensor–time–frequency space are shown for the positive and the negative mood conditions. Additionally the cluster for the mood–SME interaction is shown. Cluster dimensions in the (A) sensor space and (B) time–frequency space. (C) Averaged cluster time courses for LR and LF items. (D) Distribution of random clusters in the cluster-based permutation test. The red line marks the position of the observed cluster. All ERS/ERD values depict percent changes from a prestimulus baseline period (−1000 to 0 ms). In (A) and (B), difference values (LR − LF) are shown. In (C), percent changes for LR and LF items are shown as separate lines. The time of the stimulus onset was at 0 ms [(B) and (C)].

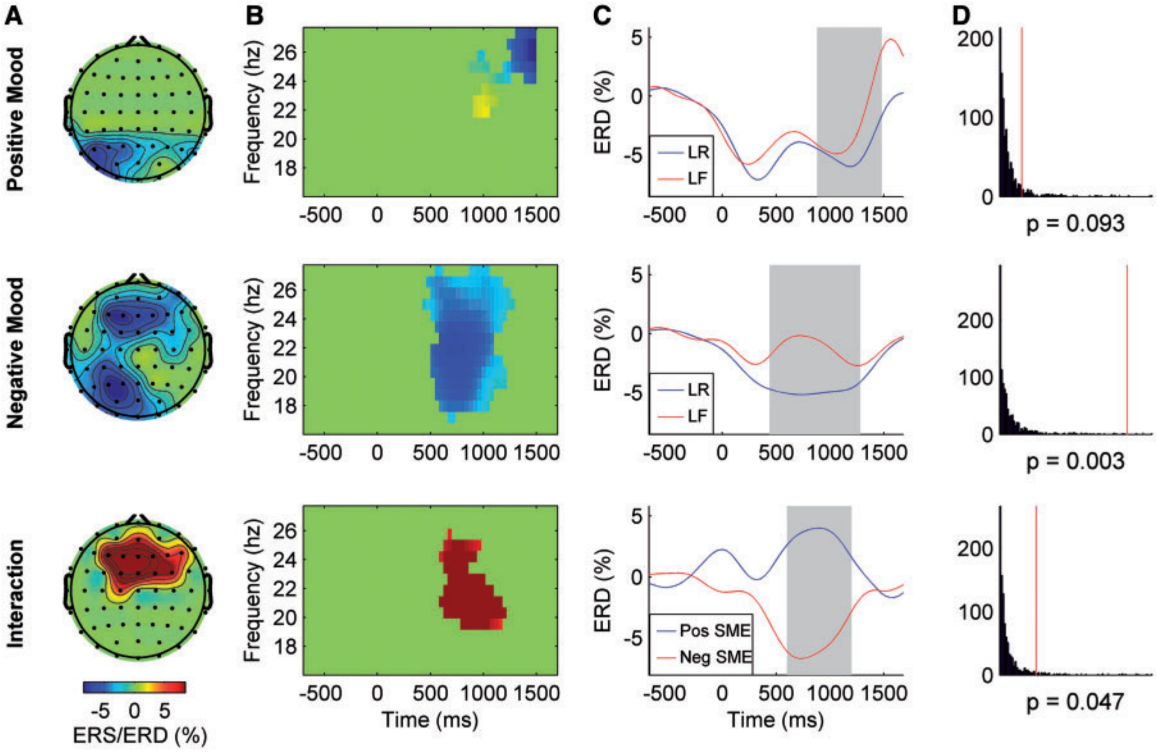

Fig. 5 Effects of mood on ERD SMEs. ERD clusters in the sensor–time–frequency space are shown for the positive and the negative mood conditions. Additionally the cluster for the mood–SME interaction is shown. Cluster dimensions in the (A) sensor space and (B) time–frequency space. (C) Averaged cluster time courses for LR and LF items. (D) Distribution of random clusters in the cluster-based permutation test. The red line marks the position of the observed cluster. All ERS/ERD values depict percent changes from a prestimulus baseline period (−1000 to 0 ms). In (A) and (B), difference values (LR − LF) are shown. In (C), percent changes for LR and LF items are shown as separate lines. The time of the stimulus onset was at 0 ms [(B) and (C)].

negative (4–8 Hz) mood. This finding could be related to the distance of the cortical regions which are involved. In fact, our results show that the SME in negative mood is located mainly in a left-frontal region, whereas the SME in positive mood is located in right-frontal and left-parietal regions. Communication between these distant regions could be related to neural synchronization in delta (2–4 Hz) oscillations. Finally, a stronger involvement of the right-hemisphere in positive mood could be attributed to the activation of larger semantic fields that might be advantageous during relational processing (Beeman *et al.*, 1994; Jung-Beeman 2005).

Processes of neural desynchronization have been linked to activation of local brain regions (Ritter *et al.*, 2009; Scheeringa *et al.*, 2011). In our study, memory formation in negative mood was specifically related to a process of neural desynchronization. This suggests a processing style that relies on the activation of specialized, local brain regions. A stimulus-driven, item-specific processing style that has been hypothesized in negative mood could rely on such activations. Encoding-related ERD in the beta band in frontal electrodes has been linked to activity in the IFG (Hanslmayr *et al.*, 2011). Our results showed that beta ERD in a frontal region was specifically linked to encoding success in negative mood. It is likely that this SME reflects IFG activation, which has been related to semantic processing of verbal material (Kim 2011). Interestingly, the IFG has also been implicated in risk aversion and inhibition in go/no-go tasks (Aron *et al.*, 2004; Christopoulos *et al.*, 2009) which could be related to the hypothesized careful encoding style in negative mood.

The ERS and ERD cluster differed substantially in their time courses. The early onset latency (0 ms) of the ERS cluster suggests that it is not directly related to the processing of incoming stimuli. Rather it is related to a state which is optimized to memorize new incoming information. Such 'memory-states' have been previously reported (Otten *et al.*, 2006; Guderian *et al.*, 2009). The onset latency (360 ms) of the ERD effect in the beta band suggests that it is related to semantic processing (Hanslmayr *et al.*, 2009). From psycholinguistic research, it is known that semantic processing of verbal material starts as early as 200 ms after stimulus onset (Pulvermüller 2001; Sereno and Rayner 2003; Hauk *et al.*, 2006; Barber and Kutas 2007).

In summary, we identified two SMEs that have both been implicated in memory formation in earlier studies. More importantly, experimentally induced mood states dissociated these effects such that successful encoding in positive mood was reflected by widespread neural synchronization in the delta band, whereas encoding success in negative mood was related to frontal desynchronization in the beta band. We conclude that processes of long-range neural synchronization in delta oscillations are related to a relational processing style, whereas frontal beta ERD is a neural correlate for an item-specific encoding style that is focused on accurate stimulus perception.

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