ERP dynamics underlying successful directed forgetting of neutral but not negative pictures

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Subjective experience suggests that negatively arousing memories are harder to control than neutral ones. Here, we investigate this issue in an item-cued directed forgetting experiment. Electroencephalogram event-related potentials (ERPs) were recorded as participants viewed un-arousing neutral and highly arousing negative photographs, each followed by a cue to remember or forget it. Directed forgetting, that is reduced recognition of ‘to-be-forgotten’ items, occurred for neutral but not negative pictures. ERPs revealed three underlying effects: first, during picture viewing a late parietal positive potential (LPP) was more pronounced for negative than for neutral pictures. Second, ‘remember’ cues were associated with larger LPPs than ‘forget’ cues. Third, an enhanced frontal positivity appeared for ‘forget’ cues. This frontal positivity was generated in right dorso-lateral prefrontal regions following neutral pictures and in medial frontal cortex following negative pictures. LPP magnitude when viewing negative pictures was correlated with reduced directed forgetting, whereas both the enhanced frontal positivity for forget cues and the larger parietal positivity for remember cues predicted more directed forgetting. This study indicates that both processes of selective rehearsal (parietal positivities) and frontally controlled inhibition contribute to successful directed forgetting. However, due to their deeper incidental processing, highly arousing negative pictures are exempt from directed forgetting.

Keywords: directed forgetting; memory; emotion; electroencephalogram; event-related potentials

INTRODUCTION

Emotionally arousing material is preferentially attended to and as a result encoded differently from neutral material (Hamann, 2001). Memories for emotional events appear more vivid (Kensinger and Corkin, 2003) and are often better remembered than memories for neutral events, at least regarding global gist (Sharot and Phelps, 2004), although not always concerning detail (Adolphs et al., 2001). Electrophysiologically, this is reflected in enhanced, parietally maximal, late parietal positive potentials (LPPs; Palomba et al., 1997). Such LPPs also occur when people are explicitly instructed to attend to (Hillyard et al., 1973) or remember (Mangels et al., 2001) certain stimuli. However, the preferential processing of emotional stimuli occurs automatically and incidentally (Dolcos and Cabeza, 2002) and everyday experience suggests that, try as we might, our ability to control encoding and prevent recall of emotional events is limited.

Yet, scientific studies of active memory suppression, involving instructions to rehearse some and actively suppress other items, such as the Think-No-Think (TNT; Anderson and Green, 2001) or the directed forgetting paradigms (Basden et al., 1993), indicate that at least healthy individuals (McNally et al., 1998; Depue et al., 2007), although perhaps not affective disorder patients (Zoellner et al., 2003; Moulds and Bryant, 2007) can actively suppress and forget emotionally negative memories. Some data even suggest more intentional forgetting of negative than neutral memories (Depue et al., 2006). However, so far most studies only varied the material’s valence, but not its arousal, comparing memory for neutral and negative words or pictures that were equally (un)-arousing. This is surprising, given that dimensional emotion theory posits that intensely negative stimuli are also high in arousal (Bradley et al., 1992) and given that the hallmark of strong-emotional memories is their associated physiological arousal (McGaugh, 2006). Indeed, the only study that varied both valence and arousal using a behavioral TNT task found highly arousing negative words to be resistant to memory suppression (Marx et al., 2008).

However, this phenomenon and its neural mechanisms have not been followed up by another TNT study with different materials or using other memory control paradigms. It is thus unclear whether and how, across different experimental situations, memory for intensely negative and therefore highly arousing material can be controlled.

Intentional memory control resulting in impaired retrieval of certain portions of presented material can be investigated using directed forgetting paradigms (Anderson, 2005; Geraerts and McNally, 2008). Whereas in the TNT paradigm differential processing of Think vs No-Think items is repeated several times, in directed forgetting paradigms the instruction to remember or forget particular items is given...
only once per item. Two varieties of directed forgetting exist, the item-method and the list-method. In the item-method, which has also often been used to investigate affective disorder patients’ ability to voluntarily control their memories (McNally et al., 1998), each individual item is followed by a cue, whereas in the list method, the cues appear after several items. While both manipulations result in reduced retrieval of to-be-forgotten information, the underlying processes are assumed to be somewhat different. The effect of item-cued directed forgetting has originally been attributed to selective rehearsal of ‘to-be-remembered’ items (Basden and Basden, 1996; Wilson and Kipp, 1998), as many behavioral studies found that item-cued directed forgetting occurs in both recall and recognition tests (Basden et al., 1993; Johnson, 1994; MacLeod, 1998). Neurophysiologically, such selective rehearsal of ‘to-be-remembered’ items should manifest in larger LPPs in response to ‘remember’ than to ‘forget’ cues.

However, in line with the concept of active suppression as also suggested for the TNT paradigm (Anderson and Green, 2001), recent neuro-scientific studies indicate that inhibitory mechanisms (Paz-Caballero and Menor, 1999; Wylie et al., 2007) are elicited by the forget cue in item-method directed forgetting.

In the electroencephalogram (EEG), such inhibitory mechanisms are supposed to be reflected in increased frontal positivities during the presentation of ‘forget’ cues (Paz-Caballero and Menor, 1999). Similarly, functional magnetic resonance imaging (fMRI) reveals distinct frontal activations for intentionally forgotten (Wylie et al., 2007) vs remembered items (Reber et al., 2002).

Evidence from the TNT task further indicates regional specialization in frontal cortex, dorso-lateral prefrontal regions supporting suppression of neutral (Anderson et al., 2004) and medio-frontal regions sub-serving suppression of negative memories (Depue et al., 2007), but the issue has not been examined in item-method directed forgetting.

Here, in an item-cued directed forgetting experiment, we investigate behavioral and neural mechanisms of memory control for highly arousing negative and un-arousing neutral items. Neutral and negative photographs are individually presented, each followed by either a ‘remember’ or ‘forget’ cue. Neutral stimuli, this procedure leads to subsequent recognition of initially ‘to-be-remembered’ than ‘to-be-forgotten’ items (Hauswald and Kessler, 2008).

Directed forgetting may be reduced for negative pictures for several reasons: under a selective rehearsal account, negative pictures may be incidentally processed more deeply already during viewing as reflected in larger LPPs. Thus, already before a cue is presented these items may be sufficiently processed, rendering further rehearsal initiated by the ‘remember’ cue (and likewise associated with LPPs) ineffective.

Under an active inhibition account, a frontal positivity should arise in response to ‘forget’ cues. This frontal positivity may differ in magnitude and regional distribution between cues following neutral and negative pictures. Since high stimulus arousal interferes with inhibitory functions (Verbruggen and De Houwer, 2007; Pessoa, 2009), inhibition of highly arousing negative memories may be less efficient than inhibition of less arousing neutral ones. If so, again, intensely negative items should be exempt from directed forgetting on a behavioral level. On a neural level, two scenarios exist: first, frontal activation elicited by forget cues following negative stimuli may be reduced, as emotion and attention compete for the same limited ‘common-pool’ resources (Pessoa, 2009). Second, since the presentation of picture and cue are temporally separated, the magnitude of frontal activity evoked by forget cues, may not differ much as a function of the preceding picture. Rather, as mentioned above, behavioral differences could be due to the negative items’ stronger pre-processing which may render inhibition efforts ineffective. This would be statistically reflected in two main effects counteracting each other: A main effect of emotional content on the LPP during picture presentation, and a main effect of cue type on the frontal positivity. The direction of correlations between parietal and frontal ERPs on the one hand and the magnitude of the behavioral directed forgetting effect on the other hand will give further insights into the ERPs functional significance.

METHODS

Subjects

Nineteen students (10 female) of the University of Konstanz (mean age: 24.74 years) participated in the experiment. Two datasets were excluded due to excessive artifacts, leaving 17 for analyses. The participants provided informed consent and received course credit or a financial compensation of €15.

Stimuli, procedure, design

The experiment was run under Presentation (Neurobehavioral Systems, Albany, USA). A set of 240 complex pictures was used (120 neutral, 120 negative). One hundred and eleven pictures were taken from the International Affective Picture System (IAPS). The remaining pictures were self-collected from the internet and had similar contents as the IAPS pictures. For all pictures normative Self-Assessment-Manikin (Bradley and Lang, 1994) ratings were available. On a scale of 1–9, valence scores were 5.23 (s.e.: 0.06) for neutral and of 2.61 (s.e.: 0.06) for negative pictures. Mean arousal was 2.82 (s.e.: 0.08) for neutral and 6.01 (s.e.: 0.06) for negative pictures. The categories differed statistically in valence \[ F(1,238) = 873.66, P < 0.001 \] and arousal \[ F(1,238) = 867.61, P < 0.001 \]. For each valence category, the pictures were organized into two paired sets.
of 60 pictures. Each picture in one set had a corresponding one with related content in the other set. Both sets of each valence were matched for arousal and valence and the pictures were digitally matched for brightness and contrast. Half of the pictures from each set were randomly assigned a ‘forget’, the other half a ‘remember’ instruction. The to-be-remembered and the to-be-forgotten items for the encoding phase were randomly drawn from one of the sets of each valence category while the corresponding pictures from the other set served as distractors in the recognition task. The assignment of the two sets was counterbalanced across subjects. Figure 1 illustrates the design.

During encoding, pictures from one neutral and one negative set were presented together in a pseudo-random consecutive sequence. Each picture was shown for 2000 ms each and was directly followed by either a ‘forget’ (F-cue, FFF) or a ‘remember’-cue (R-cue, RRR) for another 2000 ms. Hereafter, a fixation cross was shown for 1500 ms before the next picture was presented. Half of the neutral and half of the negative pictures were followed by an F-cue. Pictures from the remaining halves were followed by an R-cue. Participants were instructed to memorize the pictures with the R-cue and to forget those with the F-cue. The pictures were shown in three blocks of 40 consecutive picture-cue pairs, after each of which a short break (7 s) where participants could blink, was given. After encoding, the participants performed a speeded digit cancellation task (d2; Brickenkamp, 1994) for 5 min as a distractor task. According to other item-method studies (Paller, 1990; Basden et al., 1993; MacLeod, 1999; Paz-Caballero and Menor, 1999; Ullsperger et al., 2000; Wylie et al., 2007; Nowicka et al., 2009), a recognition task was subsequently administered as retrieval test. All 120 pictures from the encoding phase and the remaining 120 corresponding new distractor pictures were presented in random order for 300 ms each. Participants had to perform an old-new recognition test on all pictures regardless of the initial forget or remember instructions. They were instructed to react as quickly and accurately as possible. Reaction time data were corrected for outliers (±2 s.d.).

EEG recording
The EEG was recorded from 65 Ag/AgCl electrodes using Neuroscan (Scan, SynAmps, Compumedics, El Paso, USA) software and hardware. Data were acquired with a sampling rate of 500 Hz and online filters of DC-100 Hz. During recording, impedances were kept below 5 kΩ and electrodes were referenced to Cz. Prior to the experiment vertical, horizontal and blink-related eye movements were recorded from each participant for later eye movement artifact correction.

Data analysis
The recorded EEG data was pre-processed using the Brain Electrical Source Analysis package (Besa®, MEGIS Software GmbH, Gräfeling, Germany). Offline, data were re-referenced to an average reference. Data were corrected for eye movements, using individual calibrations and a topographic correction algorithm as implemented in BESA (Ille et al., 2002) and remaining large artifacts were rejected (EEG > 220 μV). For analysis of picture-evoked neural activity, the artifact-corrected data were band-pass filtered from
0.3 to 30 Hz, split into epochs (−100 to 1000 ms), baseline corrected using a 100 ms pre-stimulus epoch, and averaged. Cue presentation followed immediately after picture presentation and pictures evoked slow potentials. In order to eliminate the influence of these picture-evoked slow waves and unambiguously investigate cue-evoked activity, cue-related data were band-pass filtered from 1 to 30 Hz. Cue-evoked data were then split into epochs (−100 to 1000 ms) and averaged. This procedure led on average to 29.5 trials for F-cues following neutral pictures, 29.3 trials for F-cues following negative pictures, 29.4 trials for R-cues following neutral pictures and 29.9 trials for R-cues following negative pictures. Trial number did not differ between the conditions. Data visualization was performed using EMEGS (ElectroMagnetic EncephaloGraphy Software®, http://www.emegs.de).

**Picture presentation**

A group of eight electrodes (C1, C2, CPz, CP3, CP4, Pz, P1, P2) was extracted for statistical analysis of late-positive potentials in response to emotional pictures in a time window from 450 to 900 ms after picture onset.

**Memory cue presentation**

An increased positivity in response to F-cues following neutral pictures was identified at frontal sensors (AFz, AF3, AF4, Fz, F1, F2, FCz, FC1, FC2) starting ~450 ms after cue onset and extending until 660 ms after cue onset. Moreover, in-line with the literature, an enhanced parietal positivity in response to R-cues between 400 and 500 ms after cue onset was analyzed using the same parietal electrode group as for picture presentation. Because visual inspection of the data suggested differences in cue-related data in P2 (160–230 ms) and P4 (340–440 ms) time windows, these were also analyzed for the frontal and parietal sensor groups.

**Minimum norm source localization**

To examine a possible differential generator structure of frontal cortical activity for F-cues following negative vs neutral pictures, the sources of the event-related difference potentials F-cue–R-cue were estimated for each valence separately using the L2-Minimum-Norm-Pseudoinverse method (L2-MNP; Hamalainen and Ilmoniemi, 1994). L2-MNP is an inverse-modeling technique applied to reconstruct the topography of the primary current underlying the electric current distribution. The L2-MNP allows the estimation of distributed neural network activity without a priori assumptions regarding the location and/or number of current sources (Hamalainen and Ilmoniemi, 1994). In addition, all possible generator sources only those exclusively determined by the measured electric current are considered. Four concentric spherical shells with evenly distributed 3 (azimuthal, polar and radial direction) × 360 dipoles were used as source model. A Tikhonov regularization parameter $k$ of 0.02 was applied. For visualization purposes, the estimated sources were projected onto the surface of an averaged brain (Montreal Brain, Montreal Neurological Institute) as implemented in EMEGS.

**Statistical analysis**

All statistical calculations were done in Statistica 6.1© (StatSoft, Inc. 2003). Post-hoc comparisons were calculated using t-tests. An alpha level of 0.05 was used for all calculations. Event-related potential (ERP) data were assessed from grouped averages of several channels to obtain spatially stable estimates of cortical activity.

**Behavioral data**

Repeated-measures ANOVAs with the within-factors instruction (F-item ~ forget items, R-item ~ remember items) and valence (neutral, negative) were calculated for hits and false alarms. To distinguish discrimination accuracy from recognition bias, further measures were calculated according to the two-high-threshold model of Snodgrass and Corwin (1988). Discrimination accuracy $(Pr = \text{Hits}-\text{false alarms})$ and recognition bias $[Br = \text{false alarms}/(1−Pr)]$ were analyzed using repeated-measures ANOVAs with the within-factors instruction (F-item, R-item) and valence (neutral, negative).

Reaction times for hits and false alarms were analyzed using repeated-measures ANOVAs with the within-factors instruction (F-item, R-item) and valence (neutral, negative).

**Electrophysiological data**

**Picture presentation.** A repeated-measures ANOVA with the factor valence (neutral, negative) was used to assess parietal brain activity reflecting spontaneous attention capture and automatic encoding between 450 and 900 ms after-picture onset. The role of differential late-parietal brain activity elicited by negative vs neutral pictures (LPP negative − LPP neutral) for directed forgetting was assessed in correlation with the behavioral directed forgetting effect (recognition rate for R- minus F-pictures).

**Cue presentation.** To assess cue-related brain activity, repeated-measures ANOVAs with the within-factors cue type (F-cue, R-cue), and valence (neutral, negative) were calculated for the parietal region between 400 and 500 ms and for the frontal region between 450 and 660 ms after-cue onset.

The functional significance of both frontal and parietal activity was assessed by correlating the ERP difference between R-cue and F-cue associated activity with the difference in recognition between R- minus F-pictures (directed forgetting effect).

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2Statistical analysis of reaction times for hits and false alarms did not reveal significant results and will therefore not be discussed further.
Cue-related frontal and parietal brain activity in P2 (160–230 ms) and P4 (340–440 ms) time windows was investigated with repeated-measures ANOVAs with the within-factors cue type (F-cue, R-cue), and valence (neutral, negative).

**RESULTS**

**Recognition performance**

Mean recognition scores are displayed in Table 1. Hit rates were higher for negative compared to neutral items [valence: \( F(1,16) = 15.022, P < 0.01 \)] and of R-items compared to F-items [instruction: \( F(1,16) = 9.626, P < 0.01 \)]. However, directed forgetting occurred selectively for neutral pictures but not for negative pictures as revealed by a valence \( \times \) instruction interaction [\( F(1,16) = 14.208, P < 0.01 \)]. Recognition performance was enhanced for neutral R-items compared to neutral F-items [\( t(17) = 5.019, P < 0.001 \)], but it did not differ between negative R- and F-items. Similarly, recognition of negative F-items was elevated compared to neutral F-items [\( t(17) = 5.798, P < 0.001 \)].

Higher false alarms occurred for negative than for neutral pictures as reflected by a valence main effect [\( F(1,16) = 9.782, P < 0.01 \)]. Instruction had no effect.

**Discrimination accuracy and recognition bias**

Mean discrimination accuracies and recognition biases are displayed in Table 1. For Pr an interaction of instruction and valence [valence: \( F(1,16) = 9.401, P < 0.01 \), Figure 2] occurred. In-line with analysis of the hit data, accuracy for neutral F-items was significantly reduced compared to both neutral R-items [\( t(17) = -3.525, P < 0.01 \)] and negative F-items [\( t(17) = -2.583, P < 0.05 \)]. Recognition accuracy did not differ between negative F- and R-items (no directed forgetting) and neutral and negative R-items.

Analysis of Br showed that participants were biased to classify R-items [instruction: \( F(1,16) = 4.523, P < 0.05 \)] as well as negative items as old [valence \( F(1,16) = 8.989, P < 0.01 \)]. For Br, the effects of instruction and valence did not interact.

**EEG data**

**Picture presentation**

Negative pictures elicited enhanced positive-going activity over parietal brain areas between 450 and 900 ms after picture onset [\( F(1,16) = 27.209, P < 0.001 \), see Figure 3]. The enhanced positivity evoked by negative compared to neutral pictures was negatively correlated \( r = -0.5, P < 0.05 \) with the behavioral effect of directed forgetting (R-items – F-items) of negative pictures. The effect of directed forgetting for negative pictures decreased with increasing positive-going parietal activity for negative pictures compared to neutral ones.

**Cue presentation**

**Frontal brain activity.** Between 450 and 660 ms cues following neutral pictures evoked more positive-going activity than cues following negative pictures [valence: \( F(1,16) = 4.530, P < 0.05 \)]. Furthermore, F-cue related activity was more positive than R-cue related activity [instruction: \( F(1,16) = 12.574, P < 0.01 \), Figure 4]. For both cues following neutral and negative pictures, the respective difference in evoked activity between F-cues and R-cues correlated with the behavioral effect of directed forgetting [neutral: \( r = 0.48, P < 0.05 \); negative: \( r = 0.49, P < 0.05 \)]. Thus, the more pronounced the frontal positivity in response to F-cues was, the bigger the effect of directed forgetting. No significant P2 and P4 effects were found.

**Parietal brain activity.** Between 400 and 500 ms post cue-onset, R-cues elicited enhanced positivity [instruction: \( F(1,16) = 4.930, P < 0.05 \), Figure 5]. Furthermore, the activity difference between neutral R-cues and neutral F-cues correlated with the behavioral effect of directed forgetting for neutral pictures \( r = 0.66, P < 0.05 \). The stronger parietal activity was in response to R-cues, the bigger the directed forgetting effect for neutral items. The correlation was

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Neutral</th>
<th>R-items</th>
<th>Negative</th>
<th>R-items</th>
</tr>
</thead>
<tbody>
<tr>
<td>F-items Pr</td>
<td>0.550 (0.046)</td>
<td>0.678 (0.049)</td>
<td>0.635 (0.056)</td>
<td>0.635 (0.043)</td>
</tr>
<tr>
<td>F-items Br</td>
<td>0.217 (0.039)</td>
<td>0.265 (0.054)</td>
<td>0.330 (0.069)</td>
<td>0.456 (0.060)</td>
</tr>
<tr>
<td>R-items Pr</td>
<td>0.641 (0.044)</td>
<td>0.767 (0.041)</td>
<td>0.782 (0.033)</td>
<td>0.806 (0.029)</td>
</tr>
<tr>
<td>R-items Br</td>
<td>0.090 (0.17)</td>
<td>0.089 (0.018)</td>
<td>0.148 (0.037)</td>
<td>0.170 (0.033)</td>
</tr>
</tbody>
</table>

![Fig. 2 Pr and Br for the two item types (neutral, negative) and instructions (F-items indicate forget; R-items indicate remember).](image-url)
not significant for cues following negative pictures. Again, neither P2 nor P4 effects were found.

DISCUSSION

This study investigated behavioral and neural mechanisms underlying item-cued directed forgetting of highly arousing negative versus un-arousing neutral pictures. Behaviorally, directed forgetting was restricted to neutral pictures. Negatively arousing pictures were resistant to directed forgetting as evident from both hit rates and discrimination accuracy data.

Electrophysiologically, three effects were found to affect directed forgetting. Enhanced LPPs occurred (i) during presentation of negative pictures and (ii) during presentation of R-cues. (iii) F-cues elicited positive potentials in frontal regions. Differential correlations point to the functional significance of these effects. Both the frontal enhancement in response to F-cues and the parietal enhancement in response to R-cues were positively correlated with directed forgetting. This indicates that both selective rehearsal of R-items and active suppression of F-items contribute to the directed forgetting effect. However, a negative correlation was found between the LPP enhancement for negative pictures during viewing, and the magnitude of directed forgetting, indicating that enhanced pre-cue stimulus processing counteracts the directed forgetting effect for high-arousing negative pictures. Thus, particularly the larger LPPs during picture presentation appear to contribute to the lack of directed forgetting for negative material.

Already during picture presentation, ERPs in response to neutral and negative stimuli differed. An LPP occurred in response to arousing negative pictures in parietal brain regions between 450 and 900 ms after stimulus onset. Increased LPPs for emotionally arousing stimuli are assumed to indicate enhanced automatic attention allocation to

![Enhanced LPP during presentation of negative vs neutral pictures.](image1)

![Frontal positive potential during F-cue presentation following negative or neutral pictures.](image2)

![Effect on the LPP during R-cue presentation.](image3)
(Hajcak et al., 2009) and encoding of (Palomba et al., 1997) highly arousing emotional stimuli, contributing to memory enhancing effects of emotion (Hamann, 2001). In the present study, while hit rates were enhanced for negative items, no discrimination advantage of negative compared to neutral to-be-remembered items occurred. This pattern is consistent with other studies showing that increased LPPs to emotional pictures are more linked to enhanced hit rates than to increased discrimination accuracy (Hajcak et al., 2006). Consistent with Windmann and Kutas (2001), negatively arousing stimuli also biased recognition. Previous data suggest that emotional arousal increases ‘gist’ based processing (Adolphs et al., 2005). In-line with the presently elevated false alarm rates for negative pictures, Corson and Verrier (2007) and Windmann and Kutas (2001) found false memories more frequently for highly arousing negative than neutral stimuli. Because in our study each studied target had a thematically similar distractor in the recognition test, such arousal-driven, gist based processing may have contributed to the response bias for negative pictures. Thus, enhanced LPPs during picture presentation point to selective processing of negative pictures, which may eliminate the directed forgetting effect as indicated by the negative correlation between LPP and directed forgetting. Greater attention devoted to negative material (Hajcak et al., 2009) and differential processing and encoding (Dolcos and Cabeza, 2002) appear to counteract subsequent cue-related processing.

Previous studies on memory suppression suggest that negative words and pictures matched to neutral items in terms of arousal can be successfully suppressed (Joormann et al., 2005; Depue et al., 2006) and some data even indicate more memory suppression of emotional stimuli (Depue et al., 2006). However, in-line with our data, a recent study (Marx et al., 2008) using the TNT paradigm, found highly arousing negative words to be resistant to memory suppression. As shown repeatedly, valence and arousal are correlated, such that increasing negativity is associated with increasing arousal (Bradley and Lang, 1994; Ito et al., 1998; Kessler et al., 2007). Consequently, attempts to match intensely negative stimuli with neutral stimuli on arousal can result in unnatural stimulus selections. Directed forgetting has been found for emotional words not explicitly matched for arousal to neutral words (McNally et al., 1999), but highly arousing negative words appear to resist suppression in the TNT task (Marx et al., 2008). For item-method directed forgetting data from our group show an effect of arousal for both valences. In a recent study, arousing positive pictures also reduced directed forgetting. Furthermore, in a different study where stimuli were not pre-selected based on normative ratings but varied freely, and arousal and valence were measured, directed forgetting was inversely correlated with arousal, but not valence ratings; the more arousing the stimulus set, the smaller the directed forgetting effect (Zwissler, B et al., submitted for publication). As proposed by McGaugh (2006), emotional arousal via activation of the amygdala and adrenaline release is needed to make ‘mild moments memorable’ and indeed, viewing arousing emotional pictures evokes increased noradrenaline levels (Codispoti et al., 2003). These findings together with the results of the present study suggest that stimulus arousal may be important in eliminating directed forgetting.

A second ERP effect, an enhanced LPP for R-cues occurred 400–500 ms after cue onset, contributed to directed forgetting regardless of the emotional content of the preceding picture. This is consistent with Paz-Caballero et al’s (2004) results, who reported more positive-going parietal ERPs in response to R-cues compared to F-cues between 300 and 600 ms. Similarly, Paller (1990) found an increased parietal positivity to R-cues between 250 and 600 ms after cue onset. Such effects have been interpreted as supporting the selective rehearsal account of directed forgetting, suggesting that the effect is due to more elaborate encoding of ‘to-be-remembered’ stimuli after cue onset. Furthermore, R-cues might have the effect of a go-signal for further processing, thereby fostering parietal positivities (Roberts et al., 1994). Accordingly, at least for R-cues following neutral pictures, we found a good correlation between the R-cue associated LPP and the directed forgetting effect.

Third, indicative of processes other than selective rehearsal, starting from 450 ms after cue presentation, F-cues were associated with a frontal positivity. This effect was independent of the content of the preceding picture, although it was slightly smaller for F-cues following negative pictures. Similar to fMRI findings for the TNT task (Anderson et al., 2004; Depue et al., 2007), a distributed source model of the cortical generators of the effect suggests that when neutral pictures preceded the F-cue, right dorso-lateral prefrontal regions were more involved, whereas after a negative picture more medial portions of the prefrontal cortex were active. Importantly, regardless of picture content, the F-cue-related frontal enhancement positively correlated with the magnitude of the directed forgetting effect, supporting an inhibitory account. The effect is consistent with other studies that found enhanced F-cue related frontal activity. For example, Paz-Caballero and Menor (1999) and Paz-Caballero et al. (2004) report an increased long-lasting positivity in frontal areas, starting 300 ms after F-cue onset. Frontal brain regions are thought to be crucial for suppression and inhibition processes (Anderson et al., 2004). For example, response withholding elicits frontal P300 components in Go-Go paradigms. This ‘NoGo’ P300 anteriorization has been interpreted as reflecting cognitive control processes (Fallgatter and Strik, 1999). Similarly, Wylie et al. (2007) who investigated fMRI correlates of item-cued directed forgetting found that frontal activities differentiated between intentional and unintentional forgetting, suggesting directed forgetting as an active process. Recent neuroimaging data also support the involvement of frontal regions in the active inhibition of episodic memory contents (Anderson et al., 2004; Kuhl et al., 2007; Wimber et al., 2008) and neurophysiologically
especially frontal positivities have been implicated in such memory inhibitions (Paz-Caballero and Menor, 1999; Ullsperger et al., 2000; Johansson et al., 2007). Thus, the present results are well in-line with other studies, and by showing a brain-behavior correlation for the frontal effect add information on the functional significance of frontal positivities in item-method directed forgetting.

Although at present the F-cue-related frontal positivity was somewhat smaller following negative than following neutral items, this difference was not significant. F-cue-driven processing was similar following negative and neutral stimuli. Theoretical accounts (Pessoa, 2009) suggest that emotion and attention compete for common pool resources, implying that emotion can interfere with inhibition. However, the present temporal separation of stimulus and inhibition cue may have resulted in less interference of the two, as indicated by the absence of an emotion by cue interaction. Picture emotionality affected the subsequent cortical state at mid-latency in that following a negative picture brain potentials were less positive-going than following a neutral picture, but this effect did not differ between the two cue-types. This suggests a shift towards somewhat more excitation and less inhibition (Rockstroh et al., 1989) induced by negative pictures.

As detailed above, we suggest an important role of stimulus arousal for the modulation of directed forgetting. At least highly arousing negative stimuli reduce directed forgetting which is consistent with previous results by Marx et al. (2008) for the TNT task and other results from our group support this thesis in item-method directed forgetting also for pleasant stimuli. Still, a formal demonstration including both positive and negative stimuli in one experiment awaits further research as in the present experiment neutral and negative items varied in both valence and arousal, and, due to capacity limitations, positive stimuli were not included. Therefore, other factors besides arousal may modulate item-method directed forgetting. For instance, Marx et al. (2008), behaviorally comparing TNT performance for high- and low-arousing positive and negative stimuli, found for arousing negative stimuli a reduction of the TNT effect, while for positive stimuli the TNT effect increased with arousal. Therefore, characteristics of the present design need to be considered: Depue et al. (2006) proposed that emotional memories have stronger representations than neutral ones, which renders these memories more accessible to cognitive control. Indeed, repeated memory suppression attempts result in successful suppression of at least low-arousing negative pictures (Depue et al., 2006, 2007). However, when, as in the present study, participants cannot prepare for suppression because arousing and un-arousing items occur unpredictably in random order, no suppression is found for arousing items (Marx et al., 2008; Norby et al., 2010), although neutral stimuli are successfully suppressed (Norby et al., 2010). Electrophysiologically, anticipatory effects on successful memory suppression have also been shown by Hanslmayr et al. (2009). Thus, successful suppression of emotional stimuli may also interact with predictability of valence (Marx et al., 2008; Norby et al., 2010). Moreover, the aforementioned studies used the TNT paradigm which differs in some aspects from item-method directed forgetting: in the TNT task, the inhibitory processes (No-Think trials) are repeated several times for each to-be-suppressed item. Forgetting-related frontal slow wave activity seems to depend on suppression repetition and occurs only after several suppression repetitions (Hanslmayr et al., 2009). In the item-method, only one F-cue is presented for each to-be-forgotten stimulus, which leads to a frontal mid-latency positivity, but as supported by an additional analysis no suppression-related slow waves were found in a one-trial item-method paradigm. Both paradigms involve active suppression of some parts of the material and selective rehearsal of other portions, leading to reduced retrieval at test. Nevertheless, they differ in some aspects which may result in somewhat different findings.

In sum, this study elucidates behavioral and neural mechanisms sub-serving item-method directed forgetting of neutral vs negative material. Data indicate that in healthy volunteers both frontal inhibition elicited by the F-cue and parietally driven selective rehearsal elicited by the R-cue contribute to directed forgetting for both negative and neutral material. Different portions of the frontal cortex appear to sub-serve attempted inhibition for neutral vs negative material, right dorso-lateral regions being active when neutral pictures are inhibited, and medial regions when participants attempt to inhibit negative pictures. However, inhibition of negative pictures fails and this appears determined by their initial automatic processing during viewing before cue onset. Previous research suggests that such automatic processing is largely due to stimulus arousal (Palomba et al., 1997). Also, in-line with other previous results (Muller et al., 2008) viewing negative pictures appears to draw resources away from the subsequent task. This is reflected in generally less positive-going frontal responses to cues after negative than after neutral pictures. Thus, perhaps oddly in-line with the laypersons intuition, due to their specific automatic processing, highly arousing negative events resist directed forgetting.

REFERENCES


The whole picture-cue epochs including a 200 ms pre-picture baseline (−200 to 4000 ms) were reanalyzed without a high-pass filter in order to assess potential cue-related slow wave activity.


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