When Remembering Causes Forgetting: Electrophysiological Correlates of Retrieval-Induced Forgetting

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People tend to forget information that is related to memories they are actively trying to retrieve. On the basis of results from behavioral studies, such retrieval-induced forgetting is held to result from inhibitory control processes that are recruited to attenuate interference caused by competing memory traces. Employing electrophysiological measures of brain activity, the present study examined the neural correlates of these inhibitory processes as they operate. The results demonstrate that sustained prefrontal event-related potentials were 1) related to whether or not selective memory retrieval was required during reprocessing of previously studied words and 2) predictive of individual differences in the amount of forgetting observed in an ensuing recall test. The present findings give support to an inhibitory control account of retrieval-induced forgetting and are in accord with the view that prefrontal regions play an important role in the selection and maintenance of relevant memory representations at the expense of those currently irrelevant.

Keywords: cognitive control, episodic memory, ERP, inhibition, prefrontal cortex

Introduction

The ubiquity of remembering in everyday life makes forgetting the perhaps most salient way in which memory may err. Although a conclusive account of forgetting remains to be specified, there is ample evidence to suggest that the very act of remembering may sometimes cause forgetting (Levy and Anderson 2002; Anderson 2003). This apparently ironic memory phenomenon has frequently been demonstrated with the retrieval-practice paradigm introduced by Anderson and others (1994). In this paradigm, participants typically learn lists of category-exemplar pairs (e.g., fruits-orange, fruits-banana) from several categories (e.g., fruits, drinks) and then practice retrieval of half of the exemplars from half of the categories (e.g., retrieving orange given the cue fruits-or____). Finally, they receive a recall test in which they are encouraged to recall all studied exemplars provided with the category names as cues.

Whereas it is not surprising that retrieval practice improves later recall of the practiced material (fruits-orange), an intriguing finding is that retrieval practice impairs recall of the unpracticed material (fruits-banana), relative to a control condition in which no retrieval practice occurs at all. This detrimental effect of retrieval—referred to as retrieval-induced forgetting (Anderson and others 1994)—occurs on tests of both episodic and semantic memory (Blaxton and Neely 1983; Bäuml 2002; Johnson and Anderson 2004) and has proven relevant in a variety of settings such as eyewitness memory (Shaw and others 1995; MacLeod 2002), false memories (Bäuml and Kuhbandner 2003; Starns and Hicks 2004), impression

formation (Macrae and McLeod 1998), and stereotype representation (Dunn and Spellman 2003; Quinn and others 2004). However, the neural mechanisms subserving this memory phenomenon have yet to be investigated.

Retrieval-induced forgetting has been attributed to inhibitory control mechanisms that are recruited to overcome interference caused by competing memory traces (Anderson and others 1994; Anderson and Spellman 1995; Anderson 2003). In general, successful memory retrieval is assumed to depend on the interaction between an externally provided or internally generated cue and stored memory traces (Tulving 1983). When a cue is associated with several traces, selective retrieval of the desired memory is facilitated by inhibiting other memory traces associated with the same cue, thereby attenuating the interference caused by these competitors. Thus, efficient retrieval practice with category-plus-stem cues (e.g., fruits-or____) would entail inhibition of category exemplars that fail to overlap with the provided stems, which ultimately makes these unpracticed exemplar traces less accessible in the ensuing recall phase. Support for such an inhibitory account of retrieval-induced forgetting comes from work showing that forgetting occurs over a wide range of memory tests, including tests of word stem completion (Anderson and others 1994, 2000; Anderson and McCulloch 1999; Bäuml and Aslan 2004), tests of recognition memory (Hicks and Starns 2004; Starns and Hicks 2004), implicit memory tests (Perfect and others 2002; Veling and van Knippenberg 2004), and tests using independent probes as retrieval cues (Anderson and Spellman 1995; Anderson 2003; Aslan and others 2006; Saunders and MacLeod 2006). It is also consistent with work showing that retrieval practice affects only unpracticed items' recall accuracy but not their response latencies (Bäuml and others 2005).

In the inhibitory account of retrieval-induced forgetting, the mechanism causing forgetting is considered to operate during the intermediate phase of the retrieval-practice paradigm. Whereas this has only been inferred so far by examining the effects of inhibitory processes on later memory performance, the present study aimed at examining the act of such processes as they operate. To this end, event-related potentials (ERPs) were used to monitor brain activity during the intermediate phase of a retrieval-practice paradigm in which reprocessing of a subset of previously studied items was manipulated. ERP measures are well suited because their temporal resolution is very high and therefore allows investigation of neural activity as it takes place (cf., Rugg and Coles 1995), potentially reflecting the time course of the inhibitory processes thought to act during selective memory retrieval.

The logic of the ERP approach requires an examination of 2 types of time-locked neural activity in the intermediate phase of

a retrieval-induced forgetting experiment, that is, retrieval practice needs to be contrasted with an appropriate baseline condition that too involves reprocessing of the studied material. Relearning provides such a condition (i.e., a second opportunity to study list items; e.g., fruits-orange). Indeed, the effect of retrieval practice mimics the effect of relearning a subset of previously studied items by strengthening the reprocessed material and improving its later recall. However, only retrieval practice but not relearning induces forgetting of the not-reprocessed material, which indicates that retrieval-induced forgetting is a recall-specific effect and that retrieval but not relearning triggers inhibitory processes on the not-reprocessed material (Bäuml 1997, 2002; Ciranni and Shimamura 1999; Anderson and others 2000; Anderson and Bell 2001; Bäuml and Aslan 2004). From an ERP perspective, relearning thus provides a perfect control condition to isolate the inhibitory, recall-specific processes of the retrieval condition. From a be-havioral perspective, relearning also provides an adequate baseline, as relearning has no detrimental effect on later recall of the not-reprocessed material and thus, in a retrieval-induced forgetting experiment, is empirically indistinguishable from the no-reprocessing-at-all condition (see above).

The rationale for the ERP analysis employed in the present study was as follows. First, any potential ERP correlate of the mechanism causing retrieval-induced forgetting should be reflected in a comparison between the relearning and retrieval-reprocessing conditions because only the latter requires selec-tive memory retrieval. Second, any ERP correlate of the in-hibitory mechanism should demonstrate sensitivity to individual differences in the amount of forgetting observed in the fol-lowing recall test. We therefore grouped participants according to their memory performance, expecting differences in ERP pattern between participants showing high and low levels of retrieval-induced forgetting. In addition, we conducted a re-gression analysis to examine whether the potential ERP indices of forgetting were predictive for individual differences in the amount of retrieval-induced forgetting.

Materials and Methods

Participants
Twenty-four healthy adults (14 females) gave informed consent before they participated in return for payment of € 10/h. They had normal or corrected-to-normal vision, were right handed as determined by self-report, and their mean age was 22 years (range: 19–27 years).

Stimuli
Word lists were formed by selecting 12 exemplars from 12 distinct semantic categories (e.g., fruits). Several published norms (Battig and Montague 1969; Scheithe and Bäuml 1995) were consulted to ensure that 7 of the words on each list were strong exemplars of the given category ("targets"; e.g., apple), whereas 5 words were weaker and less typical exemplars ("nontargets"; e.g., kiwi). Because previous work provided evidence that categories' high-frequency exemplars may be more susceptible to retrieval-induced forgetting than categories' low-frequency exemplars (Anderson and others 1994; Bäuml 1998; Shivde and Anderson 2001), for each selected category, the exemplars with the higher word frequency were used as the target items (not reprocessed in the intermediate phase), and the exemplars with the lower word frequency were used as the nontarget items (reprocessed in the intermediate phase). Across category lists, the mean rank order was 11.8 for targets and 31.9 for nontargets. The initial letter of each list word was unique within the word's category.

Design and Procedure
Type of reprocessing (relearning, retrieval) was manipulated within subjects across 2 experimental blocks. In each of the 2 blocks, par-ticipants studied and recalled 6 of the category lists in a sequential manner. The trial structure for all lists was the same and consisted of a study phase, an intermediate phase, and a test phase. Whereas both study and test phases were identical for all lists across the 2 blocks, the intermediate phase varied according to the specific reprocessing requirement of a given block. In the relearning condition, the nontarget words were re-exposed for additional learning; in the retrieval condi-tion, the nontargets were presented as word stems, and participants were instructed to retrieve the corresponding study-list word. The pre-sentation order of the category lists and the assignments of lists to con-dition and condition to block were counterbalanced across participants.

Each study phase began with the explicit instruction to memorize the list words for the upcoming cued recall task. Following a 3-s pre-sentation of the category label, list items were presented for 1 s in random order with a 3-s interstimulus interval. Study phases ended with a distracter task in which participants were given 3-digit numbers and instructed to order the digits ascendingly (for approximately 30 s).

The intermediate phases started with a condition-specific instruction: "Please relearn/retrieve the following words" that was followed by a 2-s reminder of the relevant category. Each trial started with a 2.5-s fixation cross (+) that was followed by a 500-ms empty screen preceding the onset of the nontarget. Nontarget words (relearning) or nontarget stems (retrieval; initial 2–3 letters padded with crosses; e.g., Ki++ for kiwi) were presented for 2 s in random order and were each followed by a 500-ms intertrial interval. To avoid muscle artifacts in the electro-physiological recordings, participants were instructed to withhold oral responses and, thus, silently relearn or covertly retrieve the nontarget words (in total 30 items per condition).

Upon completion of the intermediate phase, participants received a cued recall test to assess their memory for the complete study list. Each test phase began with a 4-s reminder of the relevant category, which was followed by a sequential presentation of the test probes. Because each word had a unique first letter, output order could be controlled by first testing participants' memory for the 7 targets (in random order) and thereafter for the 5 nontargets. Each test trial began with a 2.5-s fixation cross that was followed by a 500-ms empty screen. The initial letter of a study word was presented for 3 s as a recall cue, and participants were told to respond orally when a question mark appeared on the screen. The experimenter coded the response as "correct" or "omission." The question mark was presented for 2 s after which the next test trial began.

The 2 experimental blocks were separated by a short subject-terminated break. The background color was set to black throughout the experiment, and stimuli and instructions were presented in white 20-pt Arial typeface at the center of a 17-in monitor. The experiment lasted approximately 2 h including application and removal of electro-des and debriefing.

Electrophysiological Methods and Analyses
The electroencephalogram (EEG) was recorded using 61 Ag/AgCl scalp electrodes referenced to the left mastoid and rereferenced off-line to the average of the left and right mastoids. Additional electrodes placed above and below the right eye and outside the outer canthi of the eyes monitored vertical and horizontal eye movements. All channels were amplified with a bandpass from DC to 100 Hz (16 bit resolution; 500 Hz sampling rate; <5 kΩ interelectrode impedance). The duration of the epochs was 2200 ms including a 200 ms prestimulus sampling period used for baseline correction. Trials containing muscle and/or recording artifacts were rejected, and trials with ocular artifacts were corrected (Gratton and others 1983) prior to averaging (with a minimum of 15 artifact-free trials per condition and participant). ERP averages were time locked to the onset of the nontarget words (relearning condition) and nontarget stems (retrieval condition) in the intermediate phases. Statistical analyses were conducted on data pooled to 8 topographic regions: anterior frontal (FP1, FPZ, FP2), left frontal (F7, F5, F3), right frontal (F4, F6, F8), left central (T7, C5, C3), right central (C4, C6, T8), left parietal (P7, P5, P3), right parietal (P4, P6, P8), and occipital (O1, OZ, O2) (see Fig. 1 for locations).
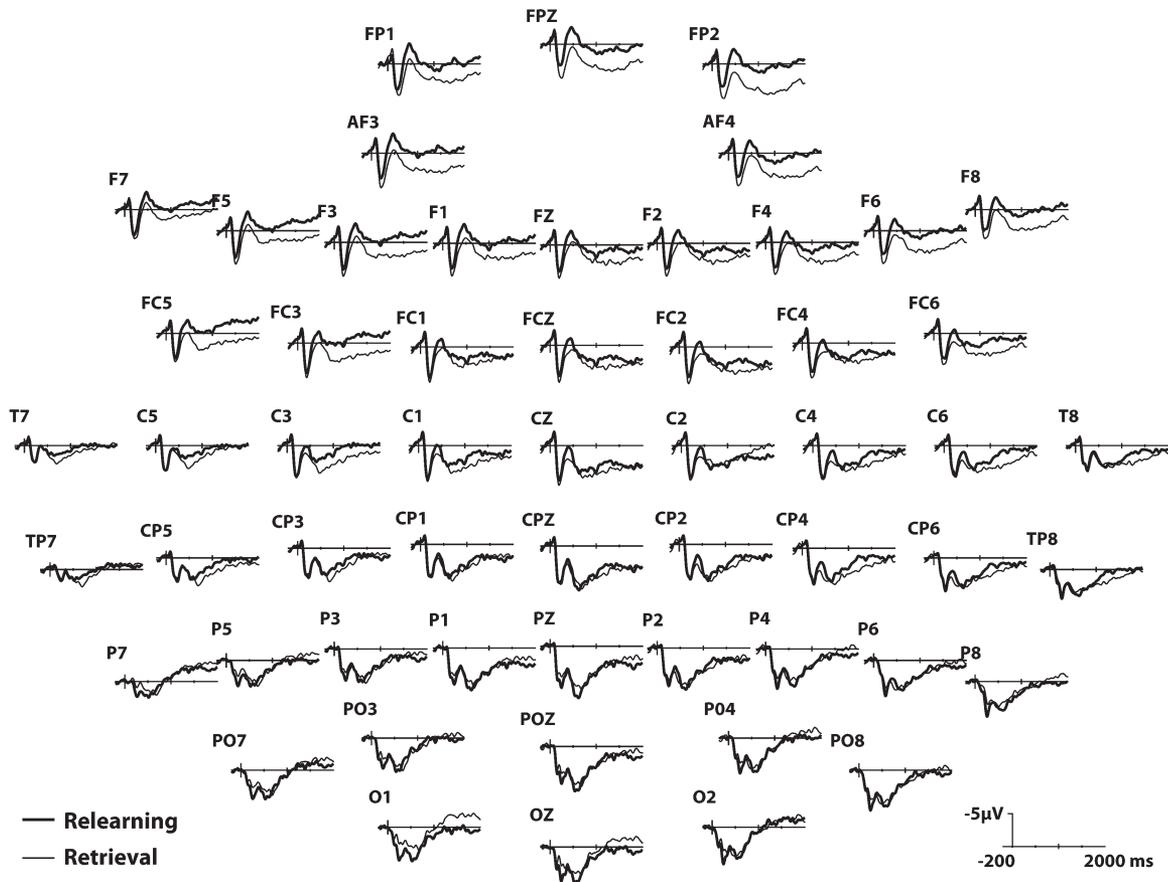
Figure 1. Grand average ERPs for nontargets in the intermediate phase as a function of reprocessing condition (relearning and retrieval). Electrodes are arranged as if looking down onto the top of the head (anterior sites at the top).

Results

Behavioral Data

An overview of participants' memory performance is given in Table 1. Target recall was significantly lower following the retrieval as compared with the baseline relearning condition (t_{23} = 2.19, P < 0.05), which demonstrates a reliable retrieval-induced forgetting effect. Type of reprocessing did not influence recall of nontargets (t_{23} = −1.09, not significant [NS]). As expected, in both the relearning and the retrieval condition, nontarget items were recalled better than target items (relearning: t_{23} = 5.02, P < 0.001; retrieval: t_{23} = 8.40, P < 0.001), indicating that the silent reprocessing during the intermediate phase was effective (the beneficial effect of retrieval on nontarget recall was only slightly larger than the beneficial effect of relearning. Whereas some previous work showed significant differences in the beneficial effects of retrieval and relearning (Carrier and Pashler 1992), in others only very small and nonsignificant differences arose (e.g., Anderson and others 2000; Bäuml and Aslan 2004). The small and nonsignificant effect in our experiment is thus well in the range of previous findings. Moreover, the smallness of the effect is indicative of the fact that, in the present experiment, relearning and retrieval were comparable in their degree of strengthening, which provides a very useful precondition for isolating the retrieval-specific inhibitory part of the ERP signal).

In a control study, we checked whether, for the material and procedure used in this experiment, the supposed equivalence

Table 1

Behavioral data in the category-plus-first-letter cued recall test

	Nontarget		Target		Forgetting index
	Relearning	Retrieval	Relearning	Retrieval	
Overall	80.3 ± 2.2	82.9 ± 2.4	68.2 ± 3.2	64.7 ± 2.9	3.5 ± 1.6
High-forgetting group	80.8 ± 3.5	81.7 ± 3.3	70.8 ± 4.0	61.1 ± 3.7	9.7 ± 0.8
Low-forgetting group	79.7 ± 2.8	84.2 ± 3.6	65.5 ± 5.1	68.3 ± 4.4	−2.8 ± 1.7

Note: Percentage (mean ± standard error of mean) of correct cued recall performance shown as a function of item type (nontarget, target) and reprocessing condition (relearning, retrieval). The forgetting index is based on target performance and calculated as relearning minus retrieval.

between the relearning and the no-reprocessing-at-all baseline condition (see above) holds true. Twenty subjects learned and recalled the same lists as described above. For one half of the lists, the nontargets were re-exposed for additional learning, for the other half, an unrelated distractor task of equal temporal duration was carried out. The EEG was not recorded. Consistent with prior work (Bäuml 1997, 2002; Ciranni and Shimamura 1999; Anderson and others 2000; Anderson and Bell 2001; Bäuml and Aslan 2004), relearning had no detrimental effect on later recall of the not-relearned target items, which was statistically indistinguishable from recall in the no-reprocessing-at-all condition (relearning: 75.5%, no-reprocessing-at-all: 77.1%; t_{19} < 1). This result further validates the use of the relearning condition as a baseline condition in the present experiment.

ERP Data

Grand averages of the ERPs elicited by nontargets in the intermediate phase are depicted in Figure 1 as a function of reprocessing condition. The primary difference between the ERPs elicited in retrieval as compared with the relearning condition is evident bilaterally over frontal regions in more positive-going ERPs in the retrieval condition. The difference onsets rather early (~200 ms) and shows a sustained time course lasting until the end of the recording epoch.

ERP waveforms were quantified by measuring the mean amplitudes in 2 consecutive time windows (early: 200–1000 ms, late: 1000–2000 ms). In the early time window, a repeated measures analysis of variance employing the factors of reprocessing (2 levels: relearning and retrieval) and region (8 levels: see Materials and Methods) revealed a reliable interaction ($F_{7,161} = 7.42$, $P < 0.001$). Subsidiary analyses showed that the difference between reprocessing conditions was confined to frontal regions (anterior: $F_{1,23} = 9.30$, $P = 0.006$; left: $F_{1,23} = 5.32$, $P = 0.030$; right: $F_{1,23} = 5.62$, $P = 0.027$). An interaction between reprocessing and region was also revealed in the later time window ($F_{1,23} = 7.54$, $P < 0.001$). Again, the retrieval condition was characterized by more positive-going ERPs than the relearning condition over frontal regions only (anterior: $F_{1,23} = 9.91$, $P = 0.005$; left: $F_{1,23} = 6.32$, $P = 0.019$; right: $F_{1,23} = 7.01$, $P = 0.014$). Measures of effect size indicated that the treatment magnitude was maximal at anterior prefrontal sites in both the early and the late time windows ($\omega^2 = 0.26$ and $\omega^2 = 0.27$, respectively).

A second set of analyses was performed to examine the functional relationship between these ERP effects and individual differences in retrieval-induced forgetting. A forgetting index was calculated (target recall; relearning minus retrieval), and a median split on this measure formed a high- and low-forgetting group of participants (see Table 1). Forgetting was significantly induced in the high-forgetting group ($t_{11} = 12.15$, $P < 0.001$) but did not reach significance in the low-forgetting group ($t_{11} = -1.68$, NS) (between-group comparison of non-target recall showed equal performance ($t_{22} < 1$, NS), indicating that reprocessing in the intermediate phase was equally beneficial for the 2 groups). ERPs in the 2 reprocessing conditions were contrasted with the between-subject factor of forgetting group (high vs. low). To control for potential item effects, we used an analysis of covariance with item counterbalancing condition as a covariate. Analyses were performed for each time window and frontal region and revealed a significant interaction between forgetting group and reprocessing in the late time window at anterior prefrontal leads ($F_{1,21} = 6.37$, $P = 0.020$). As is evident from Figures 2 and 3, the interaction reflected a larger difference between reprocessing conditions in the high-forgetting group than in the low-forgetting group between 1000 and 2000 ms after onset of the reprocessing cue ($F_{1,11} = 23.49$, $P = 0.001$ and $F_{1,11} < 1$, NS, respectively).

A complementary analysis examined whether the potential ERP indices of forgetting were predictive of individual differences in retrieval-induced forgetting, using the forgetting index as a continuous variable. Frontal amplitudes (anterior, left, right) in the early and late time windows for the relearning and retrieval conditions were subjected to a stepwise regression analysis, using as stepping criteria $P < 0.05$ for entry and $P > 0.10$ for removal. The resulting model only retained late anterior frontal ERPs elicited in the retrieval condition, which alone
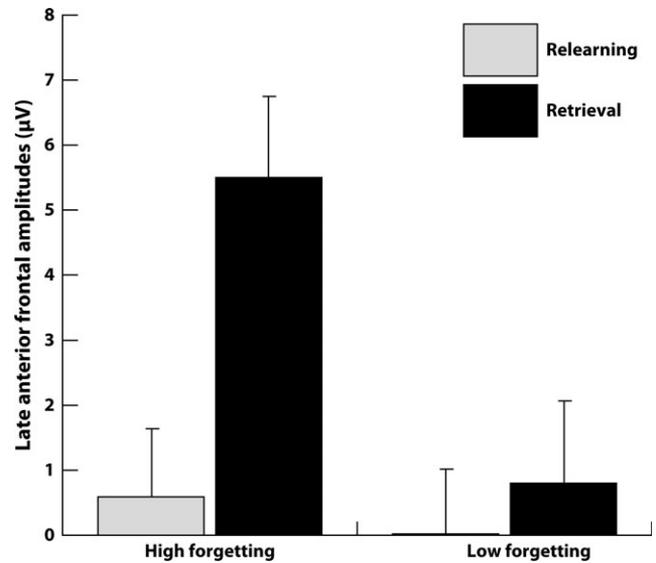

Figure 2. Anterior frontal amplitudes in the late time window (1000–2000 ms) as a function of reprocessing condition and magnitude of forgetting (high- and low-forgetting participants).
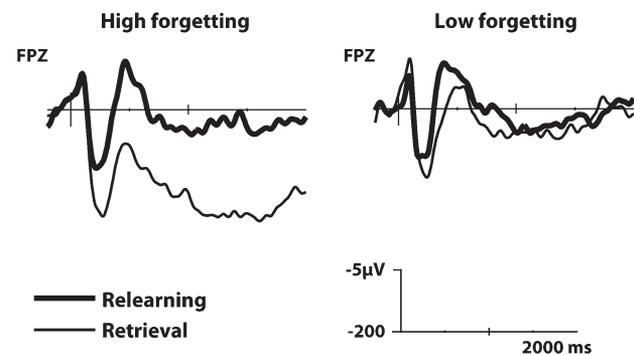
Figure 3. ERPs elicited at an anterior frontal site in the relearning and retrieval condition as a function of the magnitude of forgetting (high- and low-forgetting participants).

accounted for 33% of the variance in later forgetting ($F_{1,23} = 12.11$, $P = 0.002$, $R^2_{Adj} = 0.33$; beta = 0.596) (the same was true when data from all topographic regions entered the analysis). Accordingly, the greater the involvement of the processes reflected in these late positive-going prefrontal amplitudes, the higher the level of observed retrieval-induced forgetting in the ensuing memory test. This is consistent with the idea that the mechanisms contributing to forgetting are active during selective retrieval but absent or markedly attenuated during the baseline relearning condition (i.e., recall specific). Thus, prefrontal ERPs elicited during the intermediate phase show promise in being signatures of the mechanisms mediating retrieval-induced forgetting.

A final exploratory analysis capitalized on the high temporal resolution of ERPs and aimed at further delineating the time course of the relationship between ERPs elicited during retrieval and the behavioral index of forgetting in the following memory test. As is evident from Figure 4, showing R^2_{Adj}-values of consecutive regression analyses of retrieval practice ERPs and forgetting, the predictive power of the electrophysiological measure is prominent over anterior frontal regions in both an
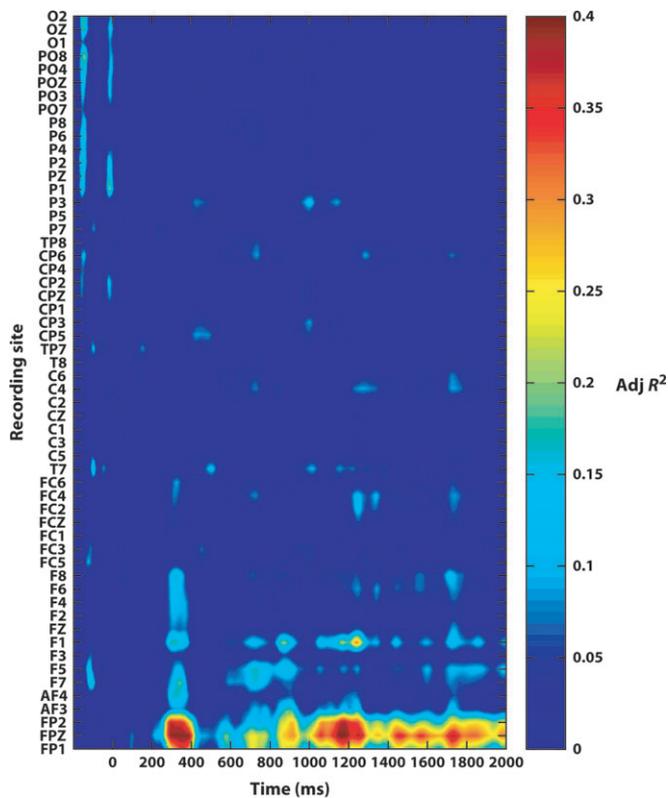
Figure 4. Predictive power (adjusted R^2) of ERPs recorded during retrieval practice for later retrieval-induced forgetting as a function of processing time and recording site.

early phasic fashion (~300–400 ms) and in a later more sustained way (~1000–2000 ms).

Discussion

To the best of our knowledge, the present study is the first to examine the electrophysiological correlates of retrieval-induced forgetting. On the basis of the results from behavioral studies, retrieval-induced forgetting is generally assumed to be due to inhibitory control recruited during selective memory retrieval to attenuate interference from competing memory traces (Anderson 2003). Addressing the neural underpinnings of the proposed mechanisms, the results of the present experiment demonstrate that ERPs recorded at prefrontal sites show condition-specific modulations during a wide window that were sensitive to whether or not forgetting of targets occurred in the ensuing cued recall task. Moreover, prefrontal ERPs elicited during the retrieval condition—the condition in which inhibitory control is thought to operate—were predictive of later retrieval-induced forgetting. Thus, these prefrontal modulations present likely candidates for ERP correlates of the inhibitory mechanisms underlying retrieval-induced forgetting.

As opposed to previous work on retrieval-induced forgetting which used overt retrieval practice in the intermediate phase (Anderson and others 1994), in the present study, we employed a covert retrieval-practice procedure. As a result, we did not have direct access to the participants' success rates in this task. It might therefore be the case that the different ERP patterns obtained for the high-forgetting and low-forgetting groups do not tap different amounts of inhibition of target items, as suggested above, but rather tap differences in (covert) retrieval

success of nontarget items. For at least 2 reasons, this is unlikely. First, differential covert retrieval during retrieval practice should be reflected in differential nontarget recall in the final test. However, although the 2 participant groups differed significantly in their level of induced forgetting, there was no such difference in nontarget recall (between-group comparison of nontarget recall showed equal performance ($t_{22} < 1$, NS), indicating that reprocessing in the intermediate phase was equally beneficial for the 2 groups). Second, prior work has shown that retrieval success in the practice phase does not predict the amount of retrieval-induced inhibition (Anderson and others 1994; MacLeod and Macrae 2001; Bäuml and Aslan 2004) and does not even appear a necessary condition for retrieval-induced forgetting (Storm and others 2005). These results from the literature together with the present pattern of target and nontarget recall suggest that the different ERP patterns obtained for the high-forgetting and low-forgetting groups actually tap differences in inhibitory function.

ERP patterns did not only differ between high- and low-forgetting groups, they were also sensitive to the kind of re-processing that were performed in the intermediate phase. In the present study, we used relearning as a baseline condition for evaluating the detrimental effect of retrieval practice. Although this choice was well motivated through the results of prior work (Ciranni and Shimamura 1999; Anderson and others 2000; Bäuml 2002), it is also consistent with the results from our control study and the ERP analysis. In fact, the ERP analysis revealed sustained and more positive-going ERPs during retrieval practice as compared with the baseline condition, which is in accord with the suggested view that only retrieval but not relearning triggers inhibitory mechanisms. Nonetheless, it would be of importance in future experiments to further examine the relationship between these prefrontal ERP modulations and retrieval-induced forgetting when the detrimental effect of retrieval practice is assessed against the standard no-reprocessing-at-all condition.

We have taken the ERP difference between relearning and retrieval to reflect the differential involvement of retrieval inhibition. Although this interpretation is consistent with the data at hand, it could be argued that there might be other processing differences between the 2 reprocessing conditions. For example, it is conceivable that the presentation of word stems in the retrieval condition calls for an active maintenance of the category cue in working memory, which is not required in the relearning condition where the exemplars are provided intact. But if the retrieval-related ERP modulation was merely a reflection of working memory, why would it predict subsequent retrieval-induced forgetting? Such an alternative explanation depends on the notion that working memory for the category cue promotes retrieval success and that this increases the probability of inhibition. However, as discussed above, there was no difference in nontarget recall as a function of the amount of induced forgetting. We therefore consider that the retrieval-inhibition account easily accommodates the present pattern of results.

Although scalp-recorded ERPs do not permit strong conclusions regarding the neuroanatomical location of their generators, on the basis of recent findings showing that sustained slow-wave activity recorded over prefrontal regions is paralleled by prefrontal activation using functional magnetic resonance imaging (fMRI) in the same experimental condition (e.g., Ranganath and Paller 1999; Ranganath and others 2000), it is

reasonable to assume that the present slow-wave pattern reflects neural activity in the prefrontal cortex. The prefrontal scalp distribution fits well with neuropsychological research suggesting a link between the integrity of prefrontal regions and resistance to memory interference (Incisa della Rocchetta and Milner 1993; Gershberg and Shimamura 1995; Shimamura and others 1995; Smith and others 1995). For example, patients with frontal lobe lesions are disproportionately impaired relative to controls during paired-associate learning when they are required to ignore previously established associations (A–B) in favor of new associations (A–C) (Shimamura and others 1995). Using a similar method to provoke proactive interference, Henson and others (2002) reported increased activity in bilateral frontopolar cortex (Brodmann's area 10) when healthy participants were cued by the first member of a pair in a "high-interference" condition relative to a control condition. The bilateral and anterior distribution of the prefrontal effect observed during selective memory retrieval in the present study is consistent with this finding.

The present results are in accord with previous work suggesting a critical role for the prefrontal regions in the control of competitor memory traces during memory retrieval (cf., Schnider 2003; Wagner and others 2004; Thompson-Schill and others 2005). Shimamura (2000) has outlined such a role in his dynamic-filtering theory of prefrontal functioning. The theory provides a general framework for understanding how prefrontal regions exert a top–down control of information processing by selecting, maintaining, updating, and rerouting information processing in posterior cortical (and subcortical) regions. With respect to the retrieval-practice paradigm employed in the present study, the prefrontal cortex may select and maintain an active representation of the task-appropriate and desired memory trace (nontarget) in the intermediate phase by gating or filtering out irrelevant memory representations (targets). Such filtering mechanisms may be particularly important when, as in the present case, competitor memory traces are strong exemplars of a given category (e.g., apple as compared with kiwi for the category fruit) and thus induce high levels of interference (Anderson and others 1994; Bäuml 1998; Shivde and Anderson 2001). The dynamic-filtering view is consistent with the ideas inherent in the inhibitory control account of retrieval-induced forgetting (Levy and Anderson 2002; Anderson 2003) and provides a compelling theoretical framework for the prefrontal involvement in the present study.

The early onset in combination with the wide temporal window in which condition- and forgetting-sensitive ERP modulations were observed here suggest that the mechanisms mediating later forgetting may act relatively promptly upon the presentation of the partial retrieval cue and show a sustained recruitment during the course of selective memory retrieval. The concluding more fine-grained time-course analysis revealed that prefrontal ERPs were especially predictive of retrieval-induced forgetting in both an early (~300–400 ms) and a late (~1000–2000 ms) time window. Given that previous ERP memory research has shown that memory retrieval starts around 300 ms following presentation of the test probe (for reviews, see Friedman and Johnson 2000; Mecklinger 2000; Rugg and Allan 2000), it is interesting to note that our data indicate that inhibitory control coincides with early memory retrieval. This is consistent with earlier work showing a concurrence of the ERP correlates of memory retrieval and control mechanisms induced by a retrieval cue (cf., Rugg and others

2000; Werkle-Bergner and others 2005) (see also Rugg and Wilding 2000) and is what would be predicted from the inhibitory control account of retrieval-induced forgetting, that is, inhibition of unwanted competitor memory traces (i.e., targets) should accompany and ease retrieval of the sought after trace (i.e., nontarget) by attenuating interference. It should be noted, however, that the present experiment used a blocked design, and thus, it is conceivable that the early-onsetting frontal ERP pattern is affected by tonic brain activity that is engaged at the outset of a retrieval-reprocessing block. Although blocking of the reprocessing conditions was appropriate in the present study in order to conform to the standard behavioral paradigm, we acknowledge that a conclusive interpretation of this early ERP pattern awaits further experimental work in which reprocessing condition is varied on a trial-by-trial basis.

Retrieval-induced forgetting reflects episodic forgetting that is mediated through the action of unintentional inhibitory processes. Interestingly, a recent study that explored intentional suppression of memory representations using fMRI revealed the activation of a bilateral dorsolateral prefrontal network that predicted later forgetting (Anderson and others 2004). Although the present results would be in accord with this finding, an important topic for future research is to assess the extent to which the same neural networks are engaged and mediate inhibition during intentional suppression as compared with selective memory retrieval.

In summary, the present study employed electrophysiological measures of brain activity to examine the neural correlates of the mechanism causing retrieval-induced forgetting. ERPs were recorded during the time at which the proposed inhibitory control mechanism is thought to operate and therefore provided information about the act of this mechanism, as opposed to only examining its impact on ensuing tests of memory. The results demonstrate that sustained prefrontal ERP waveforms were related both to whether or not selective memory retrieval was required during reprocessing of the list words and to the magnitude of later retrieval-induced forgetting. The present pattern of findings thus supports an inhibitory-control account of retrieval-induced forgetting and converges with previous neuropsychological and neuroimaging research to suggest a high relevance of prefrontal regions in the selection and maintenance of relevant memory representations at the expense of those currently irrelevant.

Notes

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