

Retrieval from Episodic Memory: Neural Mechanisms of Interference Resolution

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Abstract

■ Selectively retrieving a target memory among related memories requires some degree of inhibitory control over interfering and competing memories, a process assumed to be supported by inhibitory mechanisms. Evidence from behavioral studies suggests that such inhibitory control can lead to subsequent forgetting of the interfering information, a finding called retrieval-induced forgetting [Anderson, M. C., Bjork, R. A., & Bjork, E. L. Remembering can cause forgetting: Retrieval dynamics in long-term memory. *Journal of Experimental Psychology: Learning, Memory & Cognition*, 20, 1063–1087, 1994]. In the present functional magnetic resonance imaging study, we investigated the neural processes underlying retrieval-induced forgetting and, in particular, examined the extent to which these processes are retrieval (i.e., selection) specific.

Participants actively retrieved a subset of previously studied material (selection condition), or were re-exposed to the same material for relearning (nonselection condition). Replicating prior behavioral work, selective retrieval caused significant forgetting of the nonretrieved items on a delayed recall test, relative to the re-exposure condition. Selective retrieval was associated with increased BOLD responses in the posterior temporal and parietal association cortices, in the bilateral hippocampus, and in the dorsolateral prefrontal cortex. Medial and lateral prefrontal areas showed a strong negative linear relationship between selection-related neural activity and subsequent forgetting of competitors. These findings suggest reduced demands on inhibitory control processes when interference is successfully resolved during early selective retrieval from episodic memory. ■

INTRODUCTION

Remembering is a selection process. Given the vast amount of information available from long-term memory (Tulving & Pearlstone, 1966), momentarily irrelevant and interfering memory traces can be coactivated, causing retrieval competition. For example, when trying to recall the name of a former classmate, we might start our memory search with the vague feeling that his first name started with an “R.” This cue is likely to activate several R-names, like “Robin,” “Ralph,” or “Randy,” which we have to keep from disturbing our search in order to successfully remember that his name was indeed “Robert.” Thus, controlled retrieval not only requires the activation of relevant memory traces, but also some degree of inhibitory control over interfering memories. The latter is assumed to be accomplished through an inhibitory mechanism that weakens irrelevant, interfering information in memory (e.g., Anderson, 2003).

It is widely agreed that the prefrontal cortex plays a key role in controlling episodic retrieval in general and resolving interference in particular (for a review, see Fletcher & Henson, 2001). First, from a neuropsychological perspective, inhibitory deficits in memory, as well as in other cognitive domains, have since long been associated with dysfunction in prefrontal circuits (Shimamura, 1994). Patients with frontal lesions usually do not show memory deficits in terms of the classical amnesic syndrome, as found after damage to the medial-temporal lobe (MTL). Rather, they have difficulties in organizing materials and in adopting efficient retrieval strategies (Incisa della Rocchetta & Milner, 1993). More specifically, damage to the frontal lobes can lead to increased interference susceptibility, probably due to difficulties in inhibiting irrelevant memory contents (Shimamura, 1994). A second line of evidence comes from imaging studies of episodic retrieval, which have repeatedly demonstrated response increases in prefrontal areas with increasing control demands. Studies that varied the presence or number of competing events in long-term memory (Sohn, Goode, Stenger, Carter, & Anderson, 2003; Henson, Shallice, Josephs, & Dolan, 2002; Herrmann et al., 2001; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001) consistently found that interference has an impact mainly on activity in prefrontal regions, with maxima most frequently found in the dorsolateral (DLPFC) and ventrolateral (VLPFC) prefrontal cortex as well as in the anterior cingulate cortex (ACC). However, these studies were not directly aimed

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at investigating inhibitory control mechanisms during the retrieval process.

A behavioral indicator of competitor inhibition can be obtained by checking memory performance for suppressed competitors on a subsequent memory test. It has repeatedly been shown that retrieving only some members of a memory set can impair later recall of related, nonretrieved memories (Anderson & Spellman, 1995; Anderson, Bjork, & Bjork, 1994). This so-called retrieval-induced forgetting (RIF) is a highly robust finding, and has been interpreted as reflecting the consequences of competitor inhibition during selective retrieval. RIF has been observed in tests of cued recall (e.g., Anderson et al., 1994), recognition memory (Spitzer & Bäuml, 2007), and even implicit memory (e.g., Veling & Van Knippenberg, 2004). Its impact has, among others, been demonstrated on semantic knowledge (e.g., Johnson & Anderson, 2004) and in some more applied contexts, like foreign language acquisition (Levy, McVeigh, Marful, & Anderson, 2007), false memories (e.g., Bäuml & Kuhbandner, 2003), eyewitness memory (e.g., MacLeod, 2002), and stereotypes in social cognition (e.g., Dunn & Spellman, 2004).

Although it seems reasonable to assume that prefrontal regions mediate inhibitory memory control, a clinical investigation of neuropsychological patients indicated that patients with frontal lesions still show intact retrieval-induced forgetting (Conway & Fthenaki, 2003). The authors argued that interference resolution in episodic memory is an automated process that might not depend on prefrontal control mechanisms because it does not require the conscious allocation of attentional resources. Consistently, like the patients with frontal lesions, both schizophrenic patients and patients suffering from Alzheimer's disease showed intact retrieval-induced forgetting (Nestor et al., 2005; Moulin et al., 2002). Concluding from these clinical results that prefrontal regions are not involved in RIF might be premature, however. Indeed, all these studies examined RIF using a free recall test. RIF as found in free recall, however, need not necessarily be due to inhibition. Because in free recall, practiced items are typically recalled before unpracticed items (Wixted, Ghadisha, & Vera, 1997), the practiced items may block recall of the unpracticed material, and thus, cause forgetting without inhibition (e.g., Anderson et al., 1994; Rundus, 1973). Such a blocking account of RIF has been rejected for young adults (e.g., Anderson, 2003), but may underlie the forgetting in clinical samples, who may show a tendency to perseverate on strong, but no longer relevant, information (e.g., Raz, 2000).

In fact, in contrast to the conclusions drawn from clinical samples, two recent studies examining the neural activity during selective retrieval in healthy subjects both revealed that competitor forgetting is related to activation in the frontal cortex. One of these studies used electrophysiological measures, demon-

strating that prefrontal event-related potential (ERP) components are predictive of the degree to which subjects show retrieval-induced forgetting (Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007). In particular, ERPs averaged over selective retrieval trials revealed a sustained retrieval-specific effect at frontal sites in high but not in low forgetting subjects, indicating that these frontal effects reflect inhibitory processes that act during selective retrieval. These results are in line with a recent fMRI study which investigated the neural correlates of inhibitory mechanisms in retrieval-induced forgetting (Kuhl, Dudukovic, Kahn, & Wagner, 2007). In this study, subjects were scanned while they repeatedly retrieved a subset of previously studied cue-word associations, assuming that the need for inhibitory control decreases over repeated retrieval trials. Indeed, reduced control demands, as reflected by a decrease in prefrontal involvement, were found to be strongly related to subsequent competitor forgetting. Consistent with the view that prefrontal mechanisms mediate RIF, the findings of the two studies suggest that neural processes operating during selective retrieval are critical for eliciting forgetting in this paradigm.

The present fMRI study had two goals. The first goal was to replicate Kuhl et al.'s (2007) basic demonstration that prefrontal selection mechanisms play a key role in RIF. The second goal was to examine more directly whether such prefrontal involvement is retrieval (i.e., selection) specific. As outlined above, competitor forgetting does not have to be retrieval specific and inhibitory in nature, but may simply result from the fact that retrieval strengthens the memory representation of the retrieved items, and thus, may block recall of the nonretrieved items on a later memory test (Williams & Zacks, 2001; Mensink & Raaijmakers, 1988). In the present study, we therefore examined the retrieval specificity of prefrontal activations found in the prior imaging work on retrieval-induced forgetting.

Similar to the previous study by Kuhl et al. (2007), BOLD activity was measured during selective retrieval practice because inhibitory mechanisms are thought to operate during this phase of the experiment. Following Johansson et al. (2007), however, we introduced a different baseline condition, in which part of the material was strengthened through extra study. Behaviorally, re-exposing subjects to a subset of previously studied items has been shown to strengthen the practiced items to the same degree as selective retrieval practice. In contrast, mere re-exposure without active selection has been shown to not induce forgetting of related material (Johansson et al., 2007; Bäuml & Aslan, 2004; Bäuml, 2002; Anderson, Bjork, & Bjork, 2000; Ciranni & Shimamura, 1999), thus indicating that mere re-exposure does not trigger inhibitory mechanisms. From a neural perspective, re-exposure can control for potential effects of repeated stimulus processing, but does not involve selection or inhibition. Thus, extra presentation

of some items provides an ideal baseline for isolating the inhibitory components of the retrieval process.

In detail, in the beginning of each run of the present experiment, subjects studied several items sharing a common semantic cue (e.g., FRUIT–Apple). All items were later tested on a final recall test. In the critical intermediate phase, a subset of the studied material was practiced, either through selective retrieval of the appropriate words (FRUIT–App___, *selection condition*), or through re-exposure to the same material for additional study (FRUIT–Apple, *nonselection condition*). We expected to replicate the results from prior behavioral work by finding similar recall levels for practiced material in the selection and nonselection conditions. More importantly, we expected to replicate the previous findings of a lower recall level for the unpracticed material in the selection condition compared to the nonselection condition (Johansson et al., 2007; Bäuml & Aslan, 2004; Anderson et al., 2000; Ciranni & Shimamura, 1999), thus demonstrating RIF.

With respect to the underlying neural processes, we expected selective retrieval to go along with activation in brain regions that have previously been associated with interference and controlled retrieval from episodic long-term memory (Rugg, Otten, & Henson, 2002; Buckner, Koutstaal, Schacter, Wagner, & Rosen, 1998). In particular, we hypothesized that competitor forgetting can be predicted by prefrontal activity during selective retrieval, as suggested by the results of Kuhl et al. (2007). Some of the regions reported in their study—namely the DLPFC, the VLPFC, and ACC—should therefore play a key role in inhibitory functioning. Based on the assumption that inhibitory processes are retrieval specific, and thus, linked to active memory selection, we hypothesized that the underlying neural processes are more involved in the selection than the nonselection condition. Accordingly, selection-related activation in the relevant regions should be related to subjects' degree of retrieval-induced forgetting.

METHODS

Subjects

Twenty-four healthy right-handed volunteers (11 men, 13 women; age 20–29 years, mean age = 23.6 years) were recruited at Regensburg University. All subjects gave their written informed consent approved by the Regensburg University Ethics Committee and received payment of €12 for participation. Two participants had to be excluded from the sample due to poor memory performance (zero remembered items in three or more runs), leaving 22 subjects for further analyses.

Task Procedures

Scanning took place on a Siemens Sonata 1.5-T scanner (Siemens, Erlangen, Germany), equipped with an eight-

channel phased array head coil (MRI Devices). Stimuli were back projected centrally onto a screen at the rear of the magnet bore and viewed via a mirror attached to the head coil. Stimuli were 144 German nouns from 12 semantic categories, drawn from several published norms (Scheith & Bäuml, 1995; Battig & Montague, 1969). Each category consisted of 12 items with unique first letters with respect to their category. Within a category, the five items with the lowest rank order (mean rank = 31.8, *SD* = 8.2) had to be practiced, whereas the seven items most strongly associated with the category (mean rank = 11.8, *SD* = 5.0) served as competitors. Strong items were chosen as competitors because prior behavioral work has shown that strong, but not weak items have the potential to interfere during retrieval practice, and consequently, need to be inhibited (Bäuml, 1998; Anderson et al., 1994). The experimental material was divided into two lists with six categories each. Lists were matched according to word length and mean rank. Assignment of list to condition was counterbalanced across subjects. Within one list, presentation order of the six categories was counterbalanced across subjects such that the mean position of each category was equal.

Because we had to keep the intertrial interval (ITI) constant during the critical practice phases, a blocked design was used to ensure that all items experienced the same degree of strengthening. With the constraint of a constant ITI, events of different types (e.g., correct and incorrect items) would need to be spaced in time to yield enough power for BOLD estimation. As this would not have left enough power to separately estimate responses to each item type, we relied on a blocked design in the present experiment.

The experiment consisted of 12 separate runs, each comprising the same serial arrangement of a study phase, followed by a practice phase, a short distracter phase, and a cued recall test. During study, 12 items from a single semantic category were displayed sequentially and in random order for 2 sec each, with a 1-sec fixation interval between items. The critical experimental manipulation took place in the subsequent practice phase, in which subjects reprocessed a subset of 5 of the previously studied 12 items in random order. In the *selection condition*, subjects were given word stems (first 2–3 letters) as retrieval cues and were asked to covertly complete the stems with the appropriate items from the study list. In the baseline condition, referred to as *nonselection condition*, subjects were re-presented five complete list items with the instruction to rehearse them for the final recall test (for a similar procedure, see Johansson et al., 2007). In both conditions, practice stimuli were shown for 3 sec with an interstimulus interval of 1 sec. To exclude short-term memory effects, the practice phase was followed by a 30-sec distracter task in which subjects ordered digits in an ascending manner. During the final memory test, scanning was

interrupted to allow subject's answers to be recorded via the local intercom system. Participants were provided with the category name and a unique first letter cue and were asked to respond with the corresponding item from the study list. Unpracticed items were always tested before practiced items to control for output order effects (e.g., Anderson et al., 1994). After each run, subjects were allowed a few seconds break, and were given a warning directly before the start of a new run.

fMRI Data Acquisition and Statistical Analyses

Functional images were acquired using a T2*-weighted EPI sequence sensitive to BOLD contrast, with a TR of 3000 msec, a TE of 40 msec, and a flip angle of 90°. Each of the 12 runs lasted for about 180 sec, which resulted in 720 whole-brain acquisitions of one subject over the whole experiment. Each volume comprised 32 contiguous axial slices with an in-plane resolution of 3.0 × 3.0 mm. The first three volumes of each session were discarded to allow tissue magnetization to reach a steady state. High-resolution T1-weighted (MP-RAGE) anatomical images were collected from each participant for visualization at the end of the experiment. Head motion was restricted by using a pillow and foam inserts.

Data preprocessing and statistical analyses were performed with the SPM2 software (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm/spm2.html) under the assumption of the General Linear Model (Friston et al., 1995). EPI images were unwarped and spatially realigned to the first image acquired in the first session. Structural and functional images were spatially normalized to a T1-weighted MNI template (Cocosco, Kollokian, Kwan, & Evans, 1997). Functional images were then resampled into 2 × 2 × 2 mm voxels and smoothed with an 8-mm FWHM isotropic Gaussian kernel.

For first-level analyses, blocked regressors were formed by convolving box-car functions over periods of interest with a canonical hemodynamic response function. Four regressors per run were modeled, each of the 12 runs starting with "fixation" (20 sec), "study" (24 sec), "distracter" (28 sec), followed by either "retrieval" or "re-exposure" (20 sec), according to condition. Our first interest concerned differential activations in blocks of selective retrieval (six blocks) compared to blocks of nonselective re-exposure (six blocks). Differences between these conditions (selection – nonselection) were estimated using linear contrasts within a subject-specific fixed-effects model, with session-specific effects and low-frequency signal components (> 128 sec) being treated as confounds. Resulting estimates were then entered into a second-level analysis with subject as a random factor. Mean differences were tested with one-sample *t* tests against the hypothesis of a zero contrast value. For brain–behavior correlations, we used a simple regression model to test for voxels where estimates for

the selection > nonselection contrast were significantly correlated with individual forgetting indices across subjects. That is, we used retrieval-induced forgetting to predict the difference between the selection and the nonselection conditions. Functional ROIs with a radius of 6 mm were created around voxels that showed the highest correlation with forgetting. For description purposes, regression statistics (correlation coefficients) were then calculated for each ROI with retrieval-induced forgetting as a regressor for mean ROI activation. No statistical tests were performed on these coefficients, as they were derived from post hoc tests.

In an additional analysis, we compared activation during practice blocks against a low-level, within-session baseline (blocks of distracter), separately for blocks of retrieval and blocks of re-exposure. This analysis was conducted because the main comparison of interest (selection > nonselection) bears the risk of missing effects due to a lack of statistical power, as the two conditions were realized in different scanning blocks. Therefore, visualization of activation related to each of the two conditions may give a more complete overview over the present dataset.

Unless otherwise specified, we report only effects surviving a statistical threshold of $p < .001$, uncorrected for multiple comparisons and comprising at least 10 adjacent voxels. For visualization of cortical activations, SPM contrast images were mapped onto the surface-based human PALS-B12 atlas in SPM2 space, using the Caret 5.51 software (Van Essen et al., 2001; <http://brainmap.wustl.edu/caret>). Anatomical labeling and the assignment of Brodmann areas to peak locations were done using the WFU Pickatlas (Wake Forest University, School of Medicine, Winston-Salem; www.fmri.wfubmc.edu/cms/software) and its implemented Talairach Daemon.

As for analyses of the behavioral data, forgetting (RIF in %) was calculated as percent difference in recall performance between unpracticed items in the nonselection condition and unpracticed items in the selection condition. This RIF index has a positive value if—in line with the inhibitory account—unpracticed items are recalled worse in the selection than in the nonselection condition. Two-tailed *t* tests ($\alpha = .05$) were performed to test forgetting against the null hypothesis of zero difference.

RESULTS

Behavioral Data

Behavioral data revealed that practice through both retrieval (selection) and re-exposure (nonselection) led to a comparable mean recall performance for practiced items. 90.5% ($SE = 1.7\%$) of the previously practiced items were recalled in the nonselection condition, and 91.1% ($SE = 1.6\%$) in the selection condition, with no significant difference between the two conditions [$t(22) =$

$-0.54, p = .60$]. In contrast, correct recall of unpracticed items was significantly worse in the selection condition ($M = 66.6\%$, $SE = 1.6\%$) than in the nonselection baseline condition ($M = 73.8\%$, $SE = 1.8\%$), resulting in an average retrieval-induced forgetting effect of 7.2% ($SE = 1.4\%$) [$t(22) = 5.15, p < .0001$] (Figure 1).

Imaging Data

Modeling blocks of selective retrieval, we observed both frontal and posterior regions that showed an increase in BOLD signal relative to blocks of nonselective re-exposure (Figure 2A, red; Table 1). This general pattern of results is consistent with previous imaging studies of long-term memory retrieval (Rugg et al., 2002; Buckner et al., 1998). Posterior activations included areas in the bilateral posterior temporal association cortices extending over the inferior ($-56 -60 -10$) and middle ($-42 -62 0$) temporal gyri (both \sim BA 37), in the left superior parietal cortex ($-34 -56 62$, \sim BA 7), in the precuneus ($-26 -66 38$, \sim BA 19), in the posterior cingulate cortex ($26 -68 14$, \sim BA 31), and in the middle occipital gyrus ($44 -70 -12$, BA 19). Prefrontal response increases during selective retrieval were found in the left medial frontal ($-12 24 44$, \sim BA 8) and inferior frontal ($-40 2 32$, \sim BA 9) cortex. In contrast, there were only two small clusters that were significantly more active during the nonselection than during the selection condition, located in the left lingual gyrus ($-16 -92 -6$, \sim BA 18) and the putamen ($-18 12 -6$; see Figure 2A, green; Table 1).

When testing the same contrast with a more liberal threshold ($p < .005$, uncorrected for multiple comparisons), we found the bilateral hippocampus ($-26 -10 -26$ and $40 -22 -14$; see Figure 2B), the right fusiform gyrus ($48 -54 -18$, \sim BA 37), and another right middle temporal ($60 -48 -12$, \sim BA 37) and left posterior cingulate ($-4 -66 14$, \sim BA 23) region to be more active during selection compared to nonselection. Additional

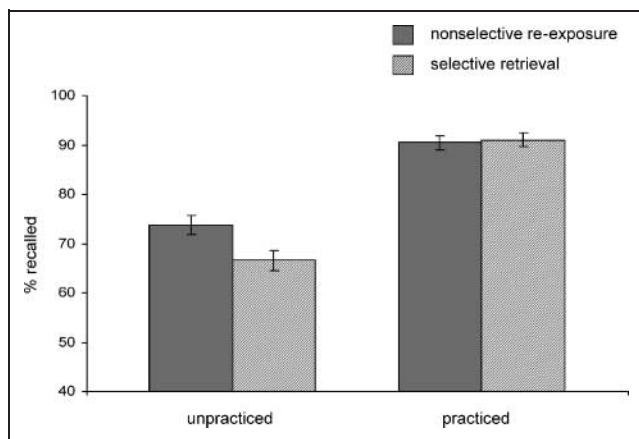


Figure 1. Behavioral performance on the final recall test: Bars correspond to mean percent correct recall and standard errors for unpracticed (left) and practiced (right) words in the selective retrieval condition compared with nonselective re-exposure.

frontal activations with this threshold were found in the left middle ($-48 22 26$, \sim BA 46; $-32 8 48$, \sim BA 6; $-38 12 42$, \sim BA 8/9 and $-52 12 44$, \sim BA 8) and inferior ($-36 36 11$, \sim BA 10/46) frontal gyrus (see Table 1). With the same liberal threshold, the reverse contrast (i.e., nonselection $>$ selection) yielded additional activation peaks in the left lingual gyrus ($-28 -78 -8$, \sim BA 18), the right putamen ($26 0 -4$), the right cingulate gyrus ($10 -30 36$, \sim BA 31), the left insula ($-36 16 6$ and $-46 6$, both \sim BA 13), and the right cuneus ($12 -86 18$, \sim BA 17).

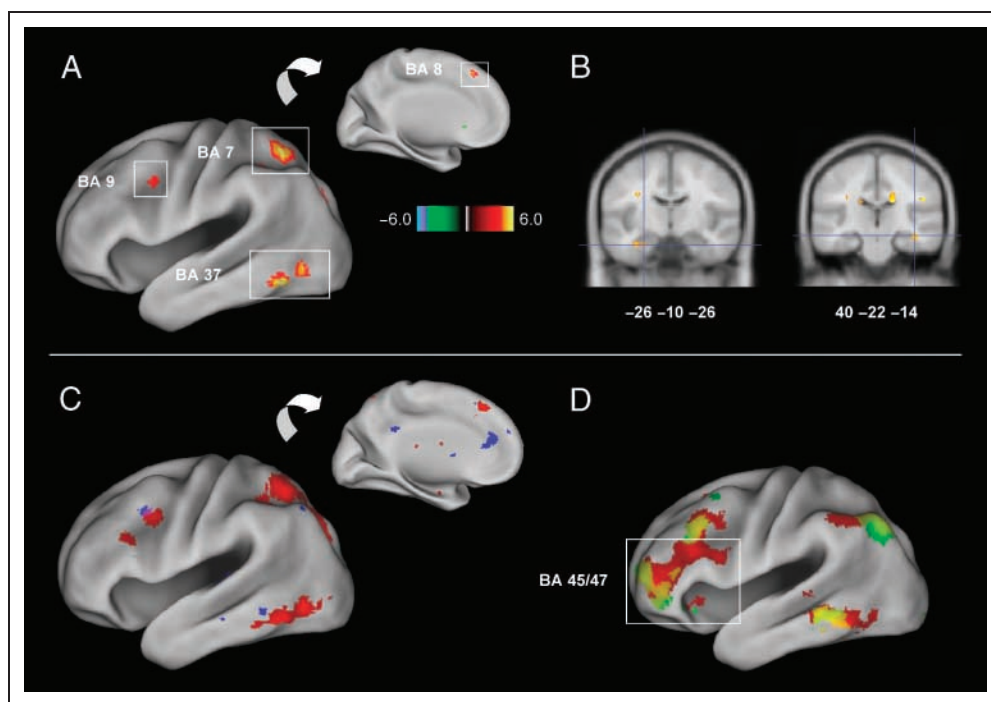
In addition to the contrast between selection and nonselection, we contrasted both conditions separately against a nonmemory activation during blocks of distracter task. The results of these contrasts are shown in Figure 2D, where red regions were activated by the selection condition, green regions by the nonselection condition, and yellow regions by both conditions (a table with a full listing of activation peaks and statistical values can be obtained on request). As can be seen from the surface overlay, the two memory conditions activated largely overlapping brain regions in the lateral prefrontal, parietal, and temporal cortices, with more extensive activation in the selection condition in all of these areas, but most pronounced in the DLPFC (BA 8/9) and VLPFC (BA 45 and 47). However, it is important to consider that differences in these areas did not survive the direct statistical comparison between conditions.

Brain–Behavior Correlations

As the main purpose of the present study was to isolate inhibitory components of the retrieval process that cause subsequent forgetting, we focused on the correlation analysis between activation patterns during selective retrieval and later forgetting. A simple regression analysis revealed that activation in some regions varied systematically with the degree of retrieval-induced forgetting (see Table 2). The two biggest clusters showing this pattern were localized in the left middle frontal cortex ($-34 16 48$ and $-44 12 40$, both \sim BA 8/9), $r = -.77$, and in ACC ($-10 34 20$, \sim BA 32), $r = -.74$, and a small cluster in a left medial frontal region ($-10 22 54$, \sim BA 6/8), $r = -.80$. All three areas showed a significant inverse relationship to individual forgetting indices (see Figure 3).

Two of the regions predicting subsequent RIF, namely, the left middle frontal cortex ($-34 16 48$ and $-44 12 40$, \sim BA 8/9) and the left medial frontal cortex ($-10 22 54$, \sim BA 6/8), seemed to be located close to areas that were found in the selection $>$ nonselection contrast ($-38 12 32$, \sim BA 8/9 and $12 24 44$, BA 8, respectively) with a threshold of $p < .005$, whereas no region in the selection $>$ nonselection contrast corresponded to the ACC ($-10 22 54$, \sim BA 32) peak that predicted forgetting. To test the degree of functional overlap between the two analyses, we built ROIs with a radius of 6 mm around voxels showing a significant ($p < .005$) effect

Figure 2. Areas showing significant activation differences between the selective retrieval and the nonselective re-exposure condition. (A) Depicted are t maps ($p < .001$, uncorrected) overlaid onto an inflated cortical surface template (Caret PALS atlas in SPM2 space). Red/yellow colors indicate regions that were significantly more active during retrieval than during re-exposure, whereas green/blue colors indicate more activation during re-exposure than during retrieval. (B) Both the left and right hippocampus showed a signal increase during selective retrieval relative to nonselective re-exposure (contrasted with a threshold of $p < .005$, uncorrected). (C) Red regions show the same contrast as in (A) with a more liberal threshold of $p < .005$, uncorrected. Blue coloring indicates regions that were negatively correlated with forgetting ($p < .005$; see also Figure 3). (D) Activation during selection (red) and nonselection (green) is contrasted separately against a low-level, within-session baseline ($p < .001$, uncorrected); yellow indicates the intersection between the two contrasts.



of selection > nonselection, and being the maxima closest to the maxima found in the correlation analysis. This yielded two ROIs, one in the left middle frontal cortex ($-38\ 12\ 32$, \sim BA 8/9) and one in the left medial frontal cortex ($-12\ 24\ 44$, \sim BA 8). Mean activity in these newly built ROIs was then tested for a significant correlation with later forgetting. Activity in the left middle frontal ROI ($-38\ 12\ 32$, \sim BA 8/9) correlated with RIF with $r = -.55$ ($p < .001$), and so did activity in the medial frontal ROI ($-12\ 24-44$, \sim BA 8, $r = -.55$, $p < .001$). The results suggest that there is substantial functional overlap between regions that show an effect of selection, and regions predicting retrieval-induced forgetting. Figure 2C shows the overlap between regions sensitive to the selection > nonselection contrast (red), and regions predicting subsequent forgetting (blue).

DISCUSSION

We adapted the standard retrieval-induced forgetting paradigm for use with functional imaging methods. This adapted paradigm allowed for BOLD measures of brain activation to be taken during phases in which inhibitory mechanisms are supposed to operate. Replicating prior behavioral work (Johansson et al., 2007; Bäuml & Aslan, 2004; Ciranni & Shimamura, 1999), practice of some members of a category improved later recall of the practiced items, regardless of whether practice occurred through selective retrieval or nonselective re-exposure; in contrast, later recall of related, but unpracticed, items

proved to be worse in the selection condition than in the nonselection condition. The latter finding is consistent with the view that processes inherent in selective retrieval trigger the suppression of competing episodes (e.g., Anderson, 2003).

Following recent work on electrophysiological correlates of RIF (Johansson et al., 2007), our experimental design did not comprise completely unpracticed categories, but rather used recall performance in the nonselection condition as a behavioral baseline. One might like to argue that forgetting in this study was present in both the selection and the nonselection condition, with forgetting in the selection condition being simply more pronounced than in the nonselection condition. Such a scenario appears unlikely, however, because results from a number of previous behavioral experiments demonstrate that the mere re-exposure of material does not induce forgetting of related, not re-exposed material, and is functionally equivalent to a no-practice condition (Bäuml & Aslan, 2004; Bäuml, 2002; Anderson et al., 2000; Ciranni & Shimamura, 1999). This finding justifies the present choice of the nonselection condition as a behavioral baseline.

Selection-related Activations in the Posterior Association Cortices and MTL

Neural models of long-term memory often describe retrieval as an interaction between posterior “storage systems” and anterior “control systems” (Rugg & Henson,

Table 1. Peak Locations Showing a Significant Effect of Selective Retrieval in the Contrast Selection (Retrieval) > Nonselection (Re-exposure), Based on the Second-level Random Effects Analysis

<i>Anatomic Label</i>	<i>BA</i>	<i>HS</i>	<i>Size</i>	<i>MNI Coordinates</i>			
				<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>
<i>Selection > Nonselection</i>							
Frontal lobe							
Medial frontal gyrus	8	L	66	-12	24	44	4.85
Middle frontal gyrus	46	L		-48	22	26	3.41*
	6	L		-32	8	48	3.40*
	8/9	L		-38	12	32	3.08*
	8			-52	12	44	2.94*
Inferior frontal gyrus	9	L	39	-40	2	32	4.17
Inferior frontal gyrus	10/46	L		-36	36	11	3.49*
Temporal lobe							
Inferior temporal gyrus	37	L	89	-56	-60	-10	5.53
Middle temporal gyrus	37	L	138	-42	-62	0	5.50
	37	R		60	-48	-12	3.40*
Fusiform gyrus	37	R		48	-54	-18	3.11*
Hippocampus	-	L		-26	-10	-26	3.28*
	-	R		40	-22	-14	3.55*
Parietal lobe							
Precuneus	7/19	L	144	-26	-66	38	5.41
Superior parietal lobe	7	L	248	-34	-56	62	4.92
Posterior cingulate	31	R	16	26	-68	14	4.50
	23	L		-4	-66	14	3.36*
Precuneus	7	L	48	-22	-75	52	4.03
Occipital lobe							
Middle occipital gyrus	19	R	44	44	-70	-12	4.61
<i>Nonselection > Selection</i>							
Lingual gyrus	18	L	38	-16	-92	-6	4.71
	18	L		-28	-78	-8	3.80*
Putamen	-	L	15	-18	12	-6	4.42
	-	R		26	0	-4	3.59*
Cingulate Gyrus	31	R		10	-30	36	3.88*
Insula	13	L		-36	16	6	3.72*
	13	L		-46	6	2	3.66*
Cuneus	17	R		16	-82	10	3.54*
				14	-86	18	3.47*

HS = hemisphere; L = left; R = right; BA = (approximate) Brodmann's area; Size = number of adjacent voxels surviving a threshold of $p < .001$.

*Additionally seen with a statistical threshold of $p < .005$.

2002; Cabeza & Nyberg, 2000; Rugg & Wilding, 2000). Involvement of lateral temporal association areas is commonly thought to reflect the activation of semantic knowledge (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Thompson-Schill, D'Esposito, & Kan, 1999; but see Noppeney, Phillips, & Price, 2004, for a discussion), so posterior temporal response increases in the present task possibly indicate spreading activation of semantic associations upon a given cue, which is the theoretical basis for interference effects in the retrieval-practice paradigm (Anderson, 2003). Parietal activation is a frequent finding in such distinct cognitive processes as attention, working memory, episodic memory, and visual perception, and it has been suggested that the typical fronto-parietal activation pattern in these tasks might reflect the integration of widespread representations stored in different neocortical areas (Naghavi & Nyberg, 2005). In episodic memory, such integrative processing might help to build up or reconstruct an integrated memory trace at the time of retrieval.

The hippocampus has been linked to binding processes and the conscious recollection of recent events (Bunge, Burrows, & Wagner, 2004; Squire, Stark, & Clark, 2004; Rugg & Yonelinas, 2003). Because only selective retrieval required the active reconstruction of past information, it may not be surprising that we found bilateral hippocampal activation associated with memory selection. Retrieval-induced forgetting occurs in the selection condition because items bound to a common cue compete for access to conscious recollection, and irrelevant competitors need to be inhibited. In contrast, no such competition is thought to occur in the nonselection condition where subjects merely engage in extra study trials. In a previous study on voluntary suppression of unwanted memories, Anderson et al. (2004) interpreted increased hippocampal activity as indicating momentary intrusions of unwanted memories that need to be inhibited. In line with this interpretation, the present finding of increased hippocampal activation in the selection condition might reflect the activation of memories that compete for conscious recollection, and confirms that the MTL plays a special role in the active reconstruction of past events.

Prefrontal Involvement in Selective Retrieval

Aside from posterior cortical regions, we also expected to find response increases in prefrontal regions. In terms of long-term memory retrieval, the prefrontal cortex is assigned a major role in guiding memory search in accordance with task-relevant features and goals (Wheeler & Buckner, 2003; Dobbins, Foley, Schacter, & Wagner, 2002). In the present study, two frontal areas showed up in the direct contrast between selective retrieval and nonselective re-exposure (see Figure 2A and Table 1), located in the medial prefrontal cortex (-12 24 44, ~BA 8) and in a caudal region of the lat-

Table 2. Peak Locations Showing a Significant Correlation with Subsequent Forgetting

Anatomic Label	BA	HS	Size	MNI Coordinates			<i>t</i>
				<i>x</i>	<i>y</i>	<i>z</i>	
<i>Frontal Lobe</i>							
Medial frontal gyrus	6/8	L	29	-10	22	54	6.87
Middle frontal gyrus	8/9	L	102	-34	16	48	6.50
				-44	12	40	4.31
Anterior cingulate	32	L	103	-10	34	20	5.22
Anterior cingulate	32	R	26	12	36	18	3.50
Medial frontal gyrus	6	R	37	10	-8	58	5.07
<i>Others</i>							
Superior temporal gyrus	41	L	58	-52	-26	4	5.13
			71	-44	-24	12	4.53
Fusiform gyrus	37	R	30	38	-48	-12	4.40
Lingual gyrus	17	L	22	-22	86	-4	4.83

HS = hemisphere; L = left; R = right; BA = (approximate) Brodmann's area; Size = number of adjacent voxels surviving a threshold of $p < .001$.

eral prefrontal cortex (-40 2 32, ~BA 9). The medial prefrontal cortex is widely agreed to be essential for processing and monitoring conflict-related information (Botvinick, Braver, Barch, Carter, & Cohen, 2001), and medial BA 8 might particularly contribute to semantic conflict processing and resolution (Van Veen & Carter, 2005). Lateral posterior prefrontal activations (BA 6/8/9/44) close to the inferior frontal junction (Derfuss, Brass, & von Cramon, 2004) have been reported in a number of tasks that involve maintaining an attentional set and selecting appropriate responses in the light of conflicting information (Derfuss et al., 2004; Bunge, Hazeltine, Scanlon, Allyson, & Gabrieli, 2002; Zysset, Müller, Lohmann, & von Cramon, 2001). Indeed, the inferior frontal junction seems to be critically involved in "controlling competing response tendencies and re-focusing attention on the currently relevant stimulus dimensions" (Zysset et al., 2001, p. 34), which exactly meets the criteria of memory selection in the face of competition. Thus, the present results, with increased BOLD signal in both the medial (BA 8) and the lateral (posterior BA 9) prefrontal cortex, might generally reflect increased demands on conflict monitoring and resolution mechanisms during memory selection.

If so, one should expect that activation in at least some of these frontal areas shows a relationship to the behavioral outcome of interference resolution, that is, to vary with the degree to which competitors show evidence of suppression on a later memory test. The results

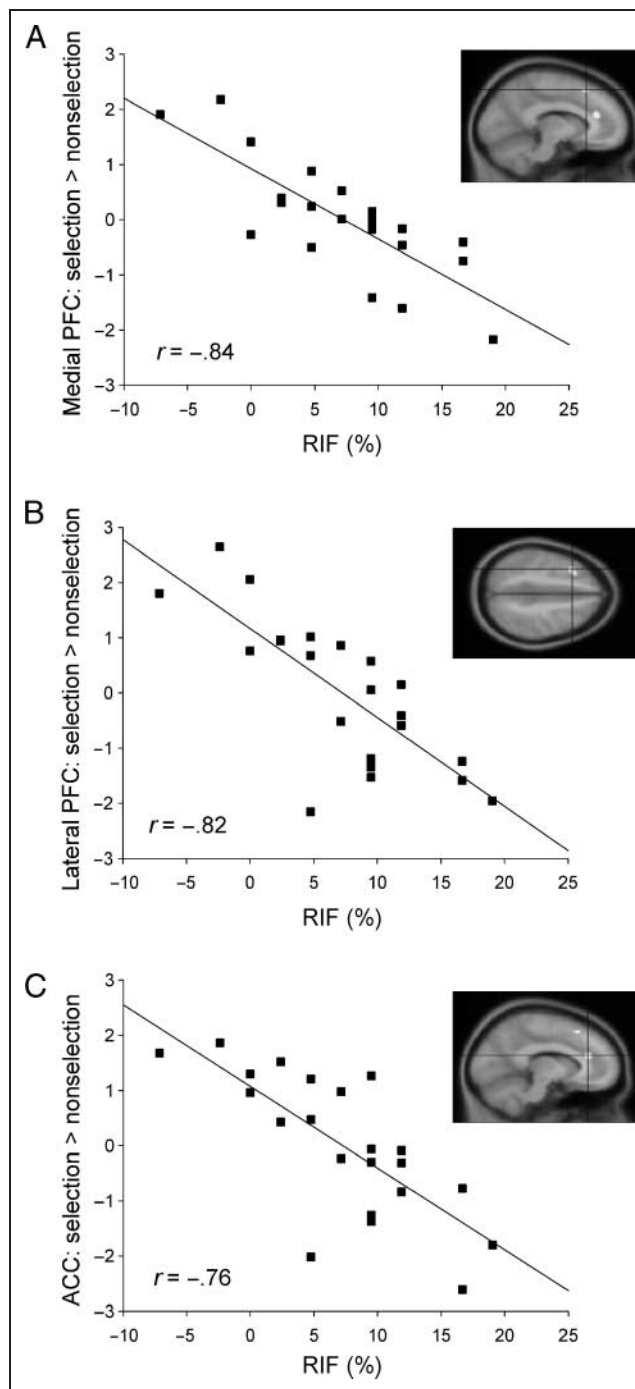


Figure 3. Regions that exhibited a significant correlation between subjects' activation during selective retrieval and their subsequent forgetting were found in (A) the medial prefrontal cortex (-10 22 54, ~BA 6/8), in (B) the left posterior prefrontal cortex (-34 16 48, ~BA 8/9), and in (C) the anterior cingulate cortex (-10 34 20, ~BA 32). Scatterplots show activation differences between the selective retrieval (selection) and the re-exposure (nonselection) condition on the y-axis (differences in beta weights), with corresponding forgetting indices (RIF in %, calculated as the difference between unpracticed items in the selection and unpracticed items in the nonselection condition) for each subject plotted on the x-axis.

of the regression analysis revealed that the strongest brain–behavior correlations were found in three prefrontal areas. These areas were located in the left medial prefrontal cortex (−10 22 54, ~BA 6/8), the left middle lateral PFC (−34 16 48, ~BA 8/9), and the left ACC (−10 34 10, ~BA 32). Maxima of the first two clusters (medial and lateral PFC) were located close to prefrontal areas found in the selection versus nonselection contrast, whereas ACC did not show up in this contrast. This functional overlap was confirmed by an additional ROI analysis. Based on the selection versus nonselection activation map, we defined two ROIs (−28 12 32, ~BA 8/9, and −12 24 44, ~BA 8) centered around the peaks closest to the voxels showing a maximal correlation with forgetting. Although these ROIs were not fully overlapping with the regions showing the brain–behavior correlations, mean activation in these ROIs significantly predicted retrieval-induced forgetting. This finding strengthens the assumption that the medial (BA 8) and lateral (BA 8/9) prefrontal areas are not only sensitive to the selection of target memories, but are also functionally linked to the inhibition of related memories. This is in line with previous findings showing that posterior medial and lateral PFC regions are related to semantic conflict resolution (Van Veen & Carter, 2005; Herrmann et al., 2001) and the representation of task-relevant features and goals (Derfuss et al., 2004).

Theoretical Implications of the Brain–Behavior Correlations

Surprisingly, all correlations between frontal activation and RIF that we identified in this study were negative in direction. A priori, one might have expected that increased competitor inhibition would be accompanied by an increase in prefrontal conflict detection and monitoring regions. The opposite pattern was found, with no area showing a positive, but several areas showing a significant negative correlation with forgetting. Two possible explanations of this finding emerge. First, subjects who are highly successful in suppressing competing items on early practice trials may need less inhibitory control on subsequent practice trials, and thus exhibit an overall decrease of inhibition-related activation over the whole retrieval practice phase, thus basically replicating the results of Kuhl et al. (2007). One possible objection to this explanation might be that, as a consequence of successful inhibition on early practice trials, subjects should experience more problems to select the remaining to-be-practiced items, as these are also successfully inhibited at first, thus predicting a positive correlation with forgetting. However, in the present study, weak (low-frequency) items were chosen as practice items (see Methods section), which are known to be less likely to interfere and to be inhibited (Bäuml, 1998; Anderson et al., 1994). Successful inhibition, therefore, should have mainly affected the competitors, and hardly

the practice items, challenging the prediction of a positive correlation between frontal activation and RIF.

A second possible explanation of the negative brain–behavior correlations arises. Subjects who are successful in inhibiting irrelevant memories might more selectively recruit the relevant brain regions, whereas less successful inhibitors recruit a broader network of frontal regions. Such fine-tuning of cortical responses has, for example, been demonstrated in developmental studies, which have shown that children recruit more extensive prefrontal regions for motor inhibition tasks than do adults (Casey, Tottenham, Liston, & Durston, 2005). Similar findings come from experiments showing that frontal regions respond more and more precisely as subjects become practiced in performing working memory tasks (e.g., Garavan, Kelley, Rosen, Rao, & Stein, 2000). With respect to the present study, this would implicate that the areas showing a negative correlation with forgetting are not relevant for inhibitory control, and are—quite the reverse—the more recruited, the less subjects manage to inhibit irrelevant and competing memories. Although this possibility cannot be completely ruled out, it seems unlikely in the light of previous findings, which provide strong evidence for a specific role of premotor (BA 6/8/32) and lateral frontal (BA 6/8/9) regions in inhibitory control, not only in motor inhibition (Garavan, Ross, Murphy, Roche, & Stein, 2002), but also in memory suppression (Anderson et al., 2004).

Implications for Selection and Inhibition in Episodic Memory

Concerning the ongoing debate on whether retrieval-induced forgetting is inhibitory or noninhibitory in nature (Perfect et al., 2004; Anderson, 2003; Williams & Zacks, 2001), the present results speak in favor of the inhibitory account of retrieval-induced forgetting. Noninhibitory accounts mostly explain RIF via mechanisms that act during the final memory test. Blocking theories, for example, posit that practicing some members of a memory set results in a final recall situation where strengthened items will come to mind more easily and block access to weaker, unpracticed items that share the same cue (e.g., Mensink & Raaijmakers, 1988). First, although blocking may cause forgetting in other contexts, its impact on the present results should be minimal, given that we found significant retrieval-induced forgetting relative to a baseline that led to equal strengthening of the practiced episodes. Also, subjects had to recall the nonpracticed items first, which typically reduces or even eliminates blocking effects (e.g., Bäuml & Aslan, 2004; Bäuml, 1997). Second, our imaging data show that prefrontal mechanisms during selective retrieval practice predict forgetting on the final recall test. Thus, the present results suggest that RIF is, indeed, retrieval specific, not strength dependent, and that the critical mechanism that causes forgetting acts during phases of selective retrieval, and not during the final

memory test. Together, the findings are in accordance with the inhibitory view on retrieval-induced forgetting.

To our knowledge, there is only one previous imaging study on retrieval-induced forgetting (Kuhl et al., 2007). These authors used an experimental setting with repeated retrieval practice on weakly associated word pairs, and used the contrast between the first and third retrieval attempt to test for decreases in cognitive control demands. Signal decreases in the left ACC and the right VLPFC over repeated retrieval attempts predicted retrieval-induced forgetting. Moreover, ACC showed some degree of functional coupling with the right superior DLPFC. Importantly, the comparison between repeated retrieval attempts is likely to include regions that are associated with the trial-to-trial strengthening of retrieved memories, or with general effects of repetition. In contrast, we specifically designed our paradigm to isolate the neural mechanisms underlying selection-specific inhibitory processes. We chose a baseline that involved strengthening of some items without inhibition of competing items, and used only one practice trial per item to exclude regions that are responsive to repeated item processing.

We basically replicated the finding of Kuhl et al. (2007) that a network of prefrontal, posterior, and medial-temporal regions is responsive to selective retrieval. We also found that activity in ACC and the DLPFC predicts forgetting of competing memories, although the DLPFC peak in the present study was left lateralized and more posterior to the one previously found to covary with ACC activity. However, similar left posterior prefrontal areas have been related to response selection (Bunge et al., 2002) and memory suppression (Anderson et al., 2004) in prior work. In contrast to previous studies on memory selection (for a review, see Badre & Wagner, 2007), we did not find the typical effect of increased left VLPFC activation in the selection condition compared to nonselection. However, contrasting selection and nonselection against a low-level baseline revealed more extensive activation in the left VLPFC during selective retrieval than re-exposure (Figure 2D), so the lack of a difference in VLPFC activation between conditions might indeed be due to a lack of statistical power of this comparison.

In the standard RIF paradigm, subjects give overt verbal responses in the retrieval practice phase. In our study, following prior work (Johansson et al., 2007), subjects were asked to covertly complete the word stems during practice to avoid movement related artifacts in the fMRI data. This implies that no behavioral measure of success or task compliance is available for practice trials, so that theoretically imaging differences between conditions might be due to differences in how successful subjects engaged in the different tasks. At least two arguments speak against such a view. First, the behavioral final recall data show that practiced items experienced the same degree of en-

hancement in the two conditions, suggesting that subjects were equally successful in performing the two tasks. Second, prior work has revealed that retrieval-induced forgetting does not depend on retrieval success during practice (MacLeod & Macrae, 2001; Anderson et al., 1994), and that even the attempt to retrieve can be sufficient to induce forgetting (Storm, Bjork, Bjork, & Nestojko, 2006). These findings make it unlikely that differences in retrieval success influenced the imaging results. The same reasoning applies to the brain-behavior correlations, where individual differences in retrieval practice success may theoretically predict the degree of retrieval-induced forgetting. However, as mentioned above, our data do not support this view, because forgetting was neither correlated with the general recall level for the practiced items, nor with the difference in the practiced items' recall level between the selection and nonselection condition. Together, these observations indicate that differences between conditions, or subjects, were not the result of differences in practice performance.

Conclusion

Our findings expand the previous literature on cognitive control processes in episodic memory by showing that selection-specific neural mechanisms are related to the forgetting of competing memories. Selective retrieval was associated with a pattern of fronto-posterior and medial-temporal activations. A strong relation to inhibitory control processes was mainly found in the prefrontal cortex. The latter finding is likely to reflect decreased demands on cognitive control if competition is successfully resolved during early retrieval attempts.

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