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# Remember the source: Dissociating frontal and parietal contributions to episodic memory

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# Remember the Source: Dissociating Frontal and Parietal Contributions to Episodic Memory

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## Abstract

■ Event-related fMRI studies reveal that episodic memory retrieval modulates lateral and medial parietal cortices, dorsal middle frontal gyrus (MFG), and anterior PFC. These regions respond more for recognized old than correctly rejected new words, suggesting a neural correlate of retrieval success. Despite significant efforts examining retrieval success regions, their role in retrieval remains largely unknown. Here we asked the question, to what degree are the regions performing memory-specific operations? And if so, are they all equally sensitive to successful retrieval, or are other factors such as error detection also implicated? We investigated this question by testing whether activity in retrieval success regions was associated with task-specific contingencies (i.e., perceived targetness) or mnemonic relevance (e.g., retrieval of source context). To do this, we used a source memory task that required discrimination between remembered targets and remembered nontargets. For a given region, the modulation of neural activity by a situational factor such as target status would suggest a more domain-general role; similarly, modulations of activity linked to error detection would suggest a role in monitoring and control rather than the accumulation of evidence from memory per se. We found that parietal retrieval success regions exhibited greater activity for items receiving correct than incorrect source responses, whereas frontal retrieval success regions were most active on error trials, suggesting that posterior regions signal successful retrieval whereas frontal regions monitor retrieval outcome. In addition, perceived targetness failed to modulate fMRI activity in any retrieval success region, suggesting that these regions are retrieval specific. We discuss the different functions that these regions may support and propose an accumulator model that captures the different pattern of responses seen in frontal and parietal retrieval success regions. ■

## INTRODUCTION

Episodic remembering involves the conscious retrieval of information about previously experienced events, including the spatial and the temporal context in which they occurred. Event-related fMRI studies of recognition memory reveal a set of cortical brain regions whose activity increases with successful episodic retrieval (Henson, Hornberger, & Rugg, 2005; Wagner, Shannon, Kahn, & Buckner, 2005; Kahn, Davachi, & Wagner, 2004; Shannon & Buckner, 2004; Weis, Klaver, Reul, Elger, & Fernandez, 2004; Wheeler & Buckner, 2003, 2004; Dobbins, Rice, Wagner, & Schacter, 2003; Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002; Donaldson, Petersen, & Buckner, 2001; Donaldson, Petersen, Ollinger, & Buckner, 2001; Konishi, Wheeler, Donaldson, & Buckner, 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; for a review, cf. Rugg, Otten, & Henson, 2002; Buckner & Wheeler, 2001). Specifically, lateral and medial parietal cortices (precuneus), posterior cingulate cortex, left dorsal MFG, and left anterior PFC consistently exhibit a greater response to old items judged to be old (hits) than to new items judged to be new (correct rejections). Although the hippocampus and the related medial-temporal lobe (MTL) structures are viewed as central to episodic retrieval (Henson, 2005; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Stark & Squire, 2000), activation in these regions has been found less consistently in fMRI investigations of retrieval success (Henson, 2005). Consequently, we were interested in learning more about how the commonly found retrieval success network areas contribute to episodic retrieval.

Many of the studies identifying retrieval success regions have used old/new item recognition tasks. According to a dual process view, recognition memory decisions are associated with two retrieval processes: recollection, which is typically characterized as an effortful search-like process that supports the retrieval of contextual information, and familiarity, a more automatic process associated with a simple assessment of trace strength (Yonelinas, 2002; Gardiner & Java, 1993; Jacoby & Dallas, 1981; Mandler, 1980; Atkinson & Juola, 1973). Recollection- and familiarity-based memory judgments have been studied with fMRI, most often with the remember/know test (Vilberg & Rugg, 2007; Wheeler & Buckner, 2004; Eldridge et al., 2000; Henson et al., 1999), but also with source retrieval tasks (Ranganath et al., 2003; Cansino et al., 2002; Dobbins et al., 2002). Using the

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remember/know test, activity in some old/new retrieval success regions has been shown to be modulated by the subjects' phenomenological experience of remembering versus knowing (Vilberg & Rugg, 2007; Wheeler & Buckner, 2004; Henson et al., 1999). For example, Wheeler and Buckner (2004; also see Henson et al., 1999) found that activity near the left intraparietal sulcus [IPS; Brodmann's area (BA) 40/39] was equivalent on R and K trials, but activity in lateral parietal areas near the supramarginal gyrus was greater on R than on K trials. Taken together, the results from these studies suggest that individual elements of the retrieval success network found during recognition memory are likely to support separable (distinct) memory processes.

Other than recollection and familiarity, what other functions might be subserved by retrieval success regions? One possibility is that regions are recruited by the demands of carrying out a complex perceptual detection task, with memory retrieval being an incidental correlate of the general processing required. For example, a recent study by Herron, Henson, and Rugg (2004) using an old/new probability manipulation suggests that some retrieval success regions are modulated by target expectancy or salience. When old items occurred more frequently than new items, the old > new retrieval success effect found in the superior parietal and frontal lobes disappeared (old = new) or reversed (new > old). An important conclusion from this study is that successful retrieval does not depend on the differential old > new activity in all areas. A different pattern of results was found in posterior retrieval success areas in or near the inferior parietal lobe, the posterior cingulate, and the precuneus. These areas were not modulated by the probability manipulation, so the differential old > new pattern of activity was present across all three probability conditions. Herron et al. hypothesized that these posterior areas are more involved in processes leading up to the old/new decision (e.g., retrieval itself). Overall, these data suggest that, at least for some retrieval success regions, activity is dependent upon expectations derived from the numbers of targets that are present during retrieval.

A number of other attempts have been made to discover whether retrieval success activity is truly related to memory rather than to nonmemory factors. For example, Shannon and Buckner (2004), focusing on the role of parietal cortex, reported a series of recognition experiments in which they controlled for response contingencies (among other factors) to investigate whether motor intention could explain the retrieval success effects. In one task, subjects were presented old and new items and only responded overtly to the old items, withholding responses for new items. In a different task, the target was switched, so that responses were only made for new items. This manipulation did not influence the retrieval success effect in parietal areas, suggesting that their function is not dependent upon explicit response contingencies. However, because this study only examined the role of parietal cortex, it is unclear whether the rest of the retrieval success network behaves similarly.

Stronger evidence for memory-specific processing in retrieval success regions per se can be found in studies that keep the requirement to retrieve constant but manipulate what is being retrieved. For example, in another recent investigation, Klostermann, Kane, and Shimamura (2008) examined whether activity in posterior parietal cortex was dependent on either the nature of the stimuli or the modality of testing. In this experiment, participants were required to remember abstract and concrete stimuli that were presented auditorily while they had their eyes closed. Again, retrieval success activity was evident in all testing conditions, suggesting that it does reflect processing related to memory retrieval per se and is not dependent on bottom–up visuospatial processing. Of course, although manipulations of retrieval content are important, in studies of this kind it is difficult to rule out the possibility that the results reflect little more than incidental variation in perceptual features (e.g., unintended differences in the processing of spatial information in the case of parietal activity).

Given their apparent ubiquity in fMRI studies, it is therefore surprising that there is only recent evidence that damage to the retrieval success structures, particularly the bilateral parietal lobes, is associated with impaired memory. For example, Berryhill, Phuong, Picasso, Cabeza, and Olson (2007) found impaired autobiographical memory in patients with bilateral superior and medial parietal lesions. The degree to which these lesions overlap with fMRI-defined retrieval success areas is difficult to assess, however, because no reference comparison was presented in their report. In contrast, a more recent report failed to find memory (recall) impairments in patients with unilateral parietal lesions (Simons et al., 2008). In this case, the locus of the lesions overlapped considerably with fMRI retrieval success activations reported in healthy control subjects, but it is unclear whether the lack of memory deficit simply reflected functioning of the undamaged hemisphere. Thus, despite the significant advances in fMRI studies of recognition memory noted above and the recent attempts to study these regions in patients, the role that frontal and parietal retrieval success regions play in memory retrieval remains largely unknown (Wagner et al., 2005). In part because of the lack of evidence that parietal damage impairs general memory processing, recent theories have posited that different areas of parietal cortex are involved in bottom–up capture and strategic top–down aspects of attention that are useful, but not imperative, for memory retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008).

The principle aim of the present experiment is to investigate further how retrieval success regions support recognition performance. In the present study, we used a source memory task because it provides a more direct index of episodic recollection than is available using the

more frequently used item recognition task (e.g., completely ruling out unconscious priming as a basis for performance). In the experiment, subjects separately studied words that were presented entirely in either red or green letters. At test, old and new words were presented in white font, and subjects were required to discriminate between targets (old words seen in one color) and nontargets (old words seen in the other color and new words) in an exclusion task (Rugg, Henson, & Robb, 2003; Jacoby, 1991). Importantly, to perform the source memory task correctly, participants must be able to both recognize studied items as old (the difference between old and new stimuli) and distinguish between different classes of studied item (the difference between targets and nontarget stimuli). To be clear, simply recognizing that an item is familiar is not sufficient to perform a source memory task; instead accurate discrimination between targets and nontargets requires the retrieval of contextual (source) information, providing a clear operational definition of episodic recollection.

Using the source memory task, we were able to carry out several distinct analyses. First, we identified retrieval success regions, by comparing correctly identified old and new items; our primary aim was to examine the behavior of these retrieval success regions in an attempt to further characterize their functional significance. We next examined the extent to which fMRI activity was modulated by the accuracy of source memory and also examined whether the status of old items as "targets" of importance modulated activity in these regions. Finally, because source memory tests are more difficult than the more typical item memory test, this task also provides an opportunity to examine memory-related errors. Thus, as a final step, we used a more exploratory approach to evaluate the pattern of time courses across the various retrieval conditions. By doing so, we were able to reveal clear differences in the role of frontal and parietal retrieval success regions.

## METHODS

### Subjects and Materials

Twenty-seven subjects (13 women; mean age = 22 years, range = 18–33 years; right-handed, native English speakers, with normal vision, and no reported neurological problems) from the Washington University community participated for a $50 payment. Informed consent was obtained in accordance with the guidelines and approval of the Washington University Human Studies Committee. Data from one subject were excluded due to excessive movement artifact. The remaining 26 subjects (13 women) had a mean age of 22 years (range = 19–33 years). Response time (RT) data were lost for two subjects, resulting in a reported $n = 24$ for RT analyses and $n = 26$ for all other analyses. Behavioral stimuli consisted of 400 nouns and verbs (four to eight letter length, mean frequency = 19.1 per million, range = 10–30 per million) selected from Kucera and Francis (1982). Mapping of stimuli to item type (old target, old nontarget, and new) was counterbalanced across subjects. Stimuli were presented in central vision, in Geneva font, and in capital letters on a black background and subtended approximately 0.5° of visual angle per letter.

### Data Acquisition

MRI data were acquired using a Siemens 1.5-T Vision System (Erlangen, Germany). T1-weighted structural images were acquired first (MP-RAGE sequence: repetition time = 9.7 msec, echo time = 4 msec, flip angle = 10°, inversion time = 20 msec, delay time = 500 msec, voxel size = 1 × 1 × 1.25 mm). Functional images were acquired using an asymmetric spin-echo echo-planar sequence sensitive to BOLD contrast (T2*; repetition time = 2.5 sec, T2* evolution time = 50 msec, voxel size = 3.75 × 3.75 mm in-plane resolution with 8-mm slice thickness). Pillows and thermoplastic facemasks minimized head movement; headphones dampened scanner noise and enabled communication. A power Macintosh computer (Apple, Cupertino, CA) and Psyscope software (Cohen, MacWhinney, Flatt, & Provost, 1993) controlled stimulus display and recorded responses from a fiber-optic keypress device. An LCD projector (AmPro model LCD-150) projected stimuli onto a screen at the head of the scanner, viewable via a mirror attached to the coil. Subjects performed four functional scans during which 110 sets of 16 contiguous slices were acquired parallel to the anterior/posterior commissure plane. The first four images in each scan allowed stabilization of longitudinal magnetization; these images were used to facilitate alignment but were excluded from analysis of the functional data.

### Behavioral Paradigm

Each of the four functional scans was preceded by an unscanned study session, during which subjects generated a unique sentence for each study word. Subjects were told that they would have to remember each word and its presented color. In each study session, 50 words were presented, half colored red and half colored green. Each word was displayed for 750 msec, followed by a fixation cross hair (+) for the remainder of the trial. The study session was self-paced; to initiate the next trial, subjects pressed one button for red words, a second button for green words. A scanned test session was then performed, in which subjects were presented with 25 old targets, 25 old nontargets, and 25 new words. All stimuli in the test phase were presented in white font, so the contextual source was absent. Thus, each subject saw a total of 100 old targets, 100 old nontargets, and 100 new words. Each word was presented for 750 msec, followed by a fixation cross (+) for the remainder of the 2.5-sec trial. The presentation onset of test items was time locked to the onset of successive whole-brain acquisitions. Jitter was included to

produce a variable interstimulus interval (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Trial order was pseudorandomized so that each type of event (old targets, old nontargets, new and fixation trials) was equally likely to follow each other (Miezin et al., 2000).

Each functional scan lasted approximately 4.6 min (110 acquisitions, 1 acquisition every 2.5 sec), separated by a 5-min break during which the next study session was performed. During the scanned test session, subjects were instructed to discriminate as quickly and accurately as possible between targets and nontargets. A single class of old item (red or green words) was designated as targets, counterbalanced across subjects, with the other class of old item and new items designated as nontargets. Responses were made using the index fingers of the left and right hands on a fiber-optic response bar, and the mapping of fingers to responses was counterbalanced across subjects. Subjects were given a short practice session (i.e., 20 items at study, 30 items at test) before the first scan to familiarize them with the procedures.

### Data Analysis

Imaging data from each subject were preprocessed to remove noise and artifacts, including (a) correction for movement within and across runs using a rigid-body rotation and translation algorithm (Snyder, 1996), (b) whole-brain normalization to a common mode of 1000 to allow for comparisons across subjects (Ojemann et al., 1997), and (c) temporal realignment (using sinc interpolation) of all slices to the temporal midpoint of the first slice, accounting for differences in the acquisition time of each individual slice. Data were then resampled into 2-mm isotopic voxels, warped into standardized atlas space (cf. Talairach & Tournoux, 1988), and smoothed with a Gaussian filter (4-mm FWHM).

Preprocessed data were analyzed using the general linear model (GLM; Miezin et al., 2000; Friston, Jezzard, & Turner, 1994) on a voxel-by-voxel basis, in which all scans were collapsed into a single time series. Statistical analyses were carried out using in-house software coded in IDL (Research Systems, Inc., ITT Visual Information Solutions, Boulder, CO). Estimates of the time course of effects were derived from the model for each response category by coding the seven time points (17.5 sec) immediately following each stimulus onset. Response categories consisted of correct and incorrect responses to each type of test item, resulting in six categories: correct target (T+), incorrect target (T−), correct nontarget (NT+), incorrect nontarget (NT−), correct new (N+), and incorrect new (N−). Factors were also coded to account for within-scan linear trend and mean signal. All effects are described in terms of percent signal change, defined as signal magnitude divided by the mean signal intensity across all scans after removing the components of linear drift and coded effects. This mean is given by the average over all scans of the intercept term of the linear trend.

Group $z$-statistical maps were derived from the GLM based on a repeated measures ANOVA approach, investigating the pattern of the hemodynamic response over time. For a single response category, this reveals regions of the brain that exhibit a temporal profile that is not flat (i.e., zero) over the analyzed period. This method does not assume the shape of the BOLD response. For comparisons between response categories, this reveals regions that exhibit different temporal profiles over the analyzed period. Our goal was to identify retrieval success regions and to determine how signal modulated according to targetness and source accuracy. Retrieval success regions were identified using a $2 \times 7$ repeated measures ANOVA with levels of correct old (T+ and NT+ combined) and correct new (N+) and seven levels of time. This analysis produced an interaction map identifying voxels in which activity on correct old and correct new trials differed over time (see Figure 1).

### ROI Criteria and Time-Course Extraction

ROIs were defined from the retrieval success map following steps described previously (Wheeler et al., 2006). Briefly, the uncorrected retrieval success image (not shown) was smoothed using a 4-mm sphere kernel. An automated algorithm searched for the location of peaks exceeding $p < .001$ significance, and those less than 10 mm apart were consolidated by averaging coordinates. A second retrieval success statistical map was computed (Figure 1) with corrections for sphericity and multiple comparisons based on Monte Carlo simulations ($p < .05$ at a 45 voxel extent; McAvoy, Ollinger, & Buckner, 2001). Regions were defined by including all voxels in the uncorrected retrieval success image that were within a 10-mm radius of each peak, then excluding voxels in that region that failed to pass multiple comparisons and sphericity corrections. The reliable peaks passing these screens are listed in Table 3.

For each response category except incorrect new items, the hemodynamic response (mean percent signal change) was extracted at each of seven poststimulus time points from each ROI. There were too few incorrect new items to provide a reliable estimate of the BOLD response, so this category was excluded from the imaging analyses. Within each ROI, signal was averaged across voxels. Following previous procedures (Wheeler et al., 2006; Wheeler & Buckner, 2004; Donaldson, Petersen, Ollinger, et al., 2001) for random-effects ROI-based statistical analysis, the estimated peak response was extracted for each region for each subject, based on the average value of the third (5.0 sec) and fourth (7.5 sec) time points. These time points were selected because they represent the peak signal change across a wide range of ROIs. Specific comparisons among peak estimates were performed using two-tailed $t$ tests. For some analyses, peak estimates were analyzed using ANOVA and post hoc Tukey honestly significant difference (HSD) comparisons.

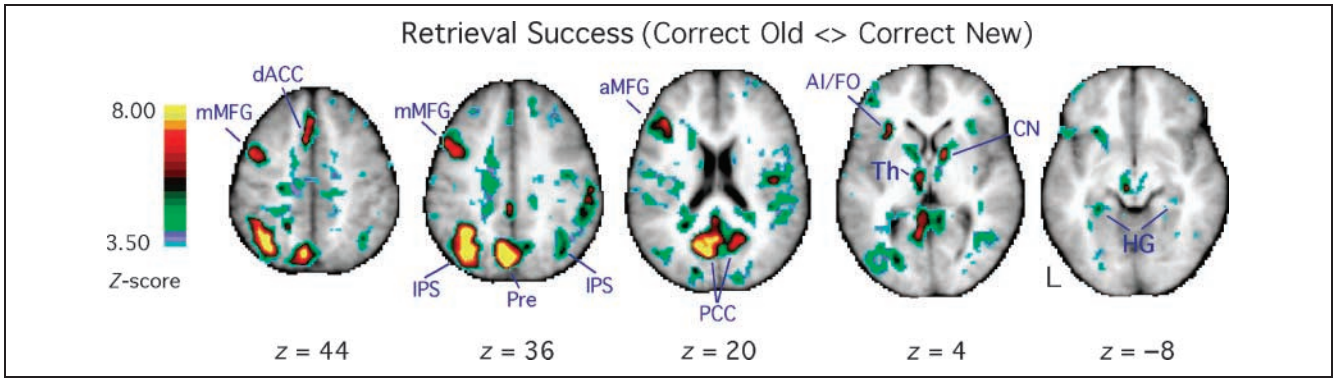


**Figure 1.** Statistical activation maps show regions of significantly greater transient activity for old items correctly judged old compared with correct new judgments. Functional maps are superimposed onto horizontally sliced structural brain images of the average anatomy. Talairach atlas *z* coordinates are listed below each slice. Significant activation peaks are listed in Tables 2 and 3. Reliability in terms of *Z* score is denoted by the color scale. AI/FO = anterior insula/frontal operculum; AG = angular gyrus; CN = caudate nucleus; dACC = dorsal anterior cingulate cortex; IPS = intraparietal sulcus; mMFG = mid-middle frontal gyrus; aMFG = anterior MFG; MTG = middle temporal gyrus; PCC = posterior cingulate cortex; Pre = precuneus; Th = thalamus; L = left hemisphere.

To determine how "source accuracy" and "targetness" modulated activity, we sorted trials using two methods. In the *source coding* approach, T+ and NT+ trials were combined into a source correct condition, whereas T− and NT− trials were combined into a source incorrect condition (Table 1). To examine activity related to the targetness criterion (*target coding*), we sorted trials instead by target accuracy (target correct and target incorrect; see Table 1).

## RESULTS

### Behavioral

Source information was accurately remembered. Under source classification, 74.3% of old items received correct judgments and 94.7% of new items were correctly rejected. RTs were significantly faster for old items receiving correct than incorrect source judgments (means of 1154 ± 128 and 1225 ± 144 msec, respectively), $t(23) = 3.98$, $p < .001$, with correct responses to new items (mean 1037 ± 122 msec) being significantly faster than source responses to old items, source correct versus correct rejection, $t(23) = 7.29$, $p < .0001$, and source incorrect versus correct rejection, $t(23) = 9.47$, $p < .0001$. Two data sets were lost due to technical problems, and one was excluded from RT analysis due to a zero false alarm rate.

When separated as a function of the target status of old items (i.e., target coding), 75.1% (*SD* = 11.9) of targets and 73.4% (*SD* = 13.8) of nontargets received correct responses. RT data were entered into a 3 × 2 ANOVA, with factors of trial type (target, nontarget, and new) and accuracy (correct and incorrect). This analysis revealed a main effect of accuracy, $F(1,44) = 28.48$, $p < .0001$), and a Type × Accuracy interaction, $F(2,44) = 12.03$, $p < .0001$, indicating that the longer RTs on incorrect trials varied as a function of trial type (see Table 2). No other effects were significant. Pairwise comparisons of correct responses revealed slower RTs to old target (1131 ± 136 msec) and old nontarget (1179 ± 130 msec) than new item trials (1037 ± 122 msec), $t(23) = 4.80$, $p < .0001$ and $t(23) = 8.85$, $p < .0001$, respectively. RTs were also slower for old nontargets than old targets, $t(23) = 2.81$ $p < .01$.

Note that chance performance is not well characterized by 50% correct; only one third of the items presented at test should receive a "target" response, and subjects must therefore overcome a strong bias toward responding "nontarget/

**Table 1.** Trial Type Designations for Source and Target GLM Coding

| *Response* | *Old Target* | *Old Nontarget* | *New* |
|---|---|---|---|
| *Item Status—Source Coding* | | | |
| Target | Source correct | Source incorrect | False alarm |
| Nontarget | Source incorrect | Source correct | Correct rejection |
| *Item Status—Target Coding* | | | |
| Target | Target correct | Miss | False alarm |
| Nontarget | Miss | Nontarget correct | Correct rejection |

**Table 2.** Mean Reaction Times (and *SD*) for Each Response Category

| *n = 23* | *New* | *Old: Target* | *Old: Nontarget* |
|---|---|---|---|
| Correct | 1036 (124) | 1126 (137) | 1173 (129) |
| Incorrect | 1283 (265) | 1241 (156) | 1214 (185) |

**Table 3.** Activation Peaks for Regions Showing a Significantly Greater Response to Correct Old (T+ and NT+) Than Correct New (N+) Trials

| *ROI* | *Hemisphere* | *Anatomic Label* | *~BA* | *x* | *y* | *z* | *Z Score* | *No. of Voxels* |
|---|---|---|---|---|---|---|---|---|
| 1 | L | Posterior precuneus | 7 | −6 | −70 | 32 | 9.4 | 526 |
| 2 | L | Inferior parietal lobule | 40 | −34 | −64 | 39 | 8.7 | 520 |
| 3 | R | Precuneus | 31 | 13 | −64 | 24 | 7.2 | 428 |
| 4 | L | Posterior cingulate | 23/30 | −6 | −56 | 11 | 7.2 | 439 |
| 5 | L | Thalamus | | −7 | −17 | 8 | 7.1 | 395 |
| 6 | L | Caudate | | −12 | 1 | 12 | 6.9 | 305 |
| 7 | L | MFG | 46/44 | −39 | 20 | 25 | 6.8 | 474 |
| 8 | R | Caudate | | 10 | 2 | 11 | 6.7 | 282 |
| 9 | L | MFG | 9 | −44 | 7 | 37 | 6.7 | 446 |
| 10 | R | Inferior parietal lobule | 40 | 55 | −27 | 32 | 6.1 | 379 |
| 11 | L | Medial frontal gyrus | 9/6 | −3 | 24 | 45 | 6.1 | 293 |
| 12 | R | Posterior cingulate | 30/23 | 10 | −54 | 11 | 6.1 | 371 |
| 13 | L | Superior frontal gyrus | 8 | −5 | 13 | 48 | 6 | 277 |
| 14 | L | White matter—tapetum | | −25 | −51 | 16 | 6 | 300 |
| 15 | R | Postcentral gyrus | 1/2 | 41 | −17 | 23 | 6 | 371 |
| 16 | R | Supramarginal gyrus | 40 | 50 | −39 | 31 | 6 | 447 |
| 17 | L | Claustrum | | −29 | 18 | 1 | 5.9 | 324 |
| 18 | L | Cingulate gyrus | 23/31 | −2 | −36 | 33 | 5.9 | 272 |
| 19 | L | MFG | 6 | −30 | −4 | 59 | 5.9 | 414 |
| 20 | R | Pyramis—cerebellum | | 35 | −68 | −31 | 5.8 | 429 |
| 21 | L | Medial frontal gyrus | 6 | −5 | 0 | 57 | 5.8 | 250 |
| 22 | L | Posterior cingulate | 23 | −3 | −43 | 25 | 5.7 | 285 |
| 23 | R | White matter—tapetum | | 19 | −43 | 16 | 5.5 | 280 |
| 24 | L | Precuneus | 7 | −19 | −50 | 47 | 5.3 | 263 |
| 25 | R | Inferior parietal lobule | 40 | 35 | −63 | 39 | 5.1 | 352 |
| 26 | L | Red nucleus | | −6 | −25 | −6 | 5.1 | 210 |
| 27 | L | White matter | | −18 | 0 | 31 | 5.1 | 309 |
| 28 | L | Cuneus | 17 | −23 | −77 | 6 | 5 | 349 |

Coordinates are listed in Talairach and Tournoux (1988) atlas space. BA is the Brodmann's area nearest to the coordinates and should be considered approximate.

new." Although it is impossible to rule out some contamination of performance by guessing, performance measures suggest that guessing was minimal. More importantly, there is no evidence for systematic differences between the responses to target and nontarget items that would complicate interpretation of the fMRI data.

### Imaging Analysis Overview

To identify retrieval success regions, we computed a voxelwise repeated measures ANOVA contrasting correct old (T+, NT+) and new (N+) trials, independently of targetness (see Methods). Regions associated with retrieval success were located in MTLs near the parahippocampal gyrus (HG), lateral parietal cortex near the IPS, medial parietal cortex near the precuneus (Pre), and left dorsolateral prefrontal (DLPF) cortex near the MFG. The retrieval success image (cf. Figure 1) also included a number of other regions that are less commonly reported: anterior insula/frontal operculum (AI/FO), dorsal anterior cingulate cortex (dACC), thalamus, posterior cingulate cortex, and caudate nucleus. Table 3 lists the most

reliably activated regions by peak coordinate and approximate BA.

### Targetness Did Not Modulate Activity in Retrieval Success Regions

To determine whether activity in retrieval success regions was related to target detection, we compared BOLD time courses on T+ and NT+ trials using repeated measures ANOVA. Targetness did not reliably modulate activity in any of the ROIs, indicating that perceived targetness was not a factor underlying retrieval success effects.

Figure 2 illustrates results from four of the retrieval success ROIs from Table 3, including mid-MFG near BA 9 (Talairach atlas $x$, $y$, $z$ peak coordinate: −44, +07, +37), anterior MFG near BA 46 (−39, +30, +25), medial parietal cortex near BA 7 (posterior precuneus; −06, −70, +36), and lateral parietal lobe near BA 40 (IPS; −34, −64, +39). Although there were clear differences in time courses between old and new items, there were no differences between T+ and T− items in any of the ROIs. To determine whether targetness modulated activity in voxels not included in the retrieval success regions, we conducted an additional exploratory voxelwise ANOVA directly contrasting T+ and T− trials. This analysis identified just one region in medial posterior parietal cortex (not shown) with differential activity between T+ and T− trials, suggesting that perceived targetness was not an important factor in retrieval modulations. Given that our primary aim is to examine the behavior of retrieval success regions behave, we do not consider this additional region further.

### Frontal and Parietal Regions Modulated Differently on Error Trials

In contrast to targetness, activity in many of the ROIs modulated according to source accuracy. Figure 3 displays results from six ROIs, including the two frontal and the two parietal ROIs displayed in Figure 2, a third frontal ROI located along posterior MFG near BA 6 (−30, −04, +59; Figure 3A), and a right parietal ROI located near right IPS (+55, −27, +32; Figure 3F).

Source accuracy did not appear to modulate activity in the left posterior MFG (Figure 3A). This observation was supported by statistical comparison of peak BOLD response estimates (averaged across time points 5.0 and 7.5 sec) of correct and incorrect source trials, $t(25) = -1.45$, $p = .16$. Activity in mid-MFG and anterior MFG ROIs appeared to increase to the same degree on incorrect and correct source trials, but with a longer duration on incorrect trials (as illustrated in Figure 3B and c, time points 5.0 and 7.5 sec). Note that the time courses show the measured data at each time point and are not fitted functions. In support of this observation, when signal changes at time points 5.0 and 7.5 sec were averaged,

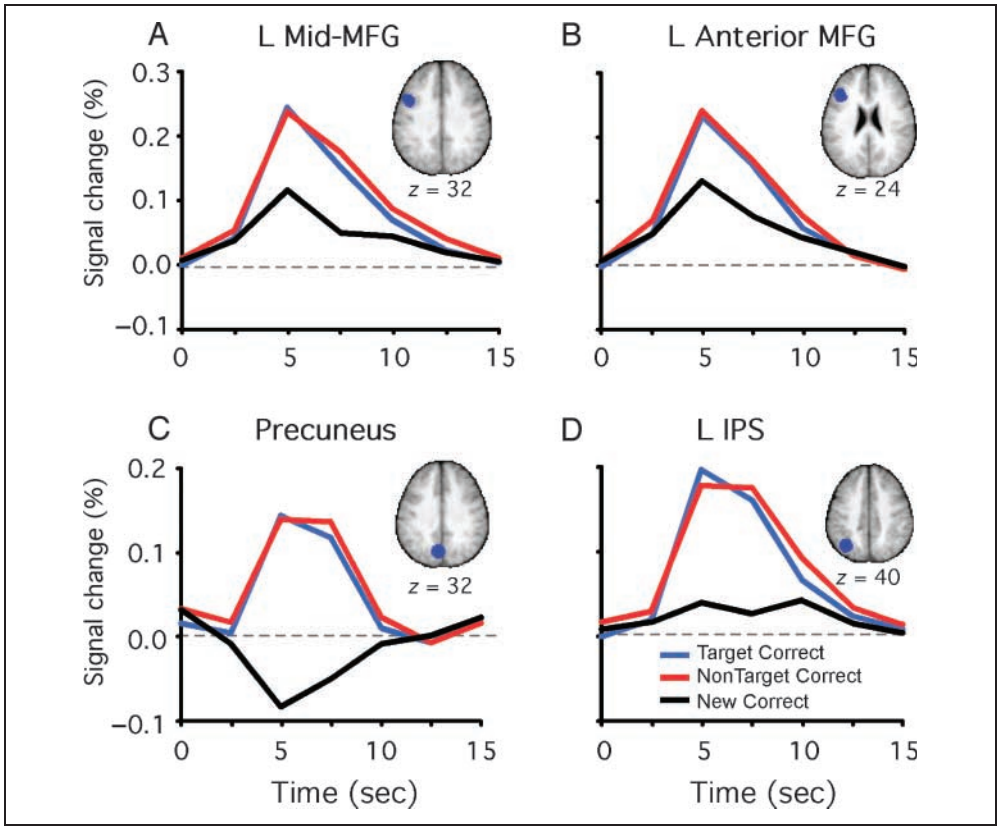


**Figure 2.** Frontal and parietal ROIs and associated time courses from the targetness analysis. ROIs include left (A) mid-middle frontal gyrus near BA 9, (B) anterior MFG near B 46, (C) precuneus near BA 7, and (d) intraparietal sulcus near BA 40 (Talairach coordinates are listed in text; see Table 3). Time courses begin at stimulus onset, denoted by time zero. Dashed horizontal lines at 0% signal change reflect baseline. Trial types are color coded according to the legend. Horizontal slice atlas coordinates are listed below each ROI image.

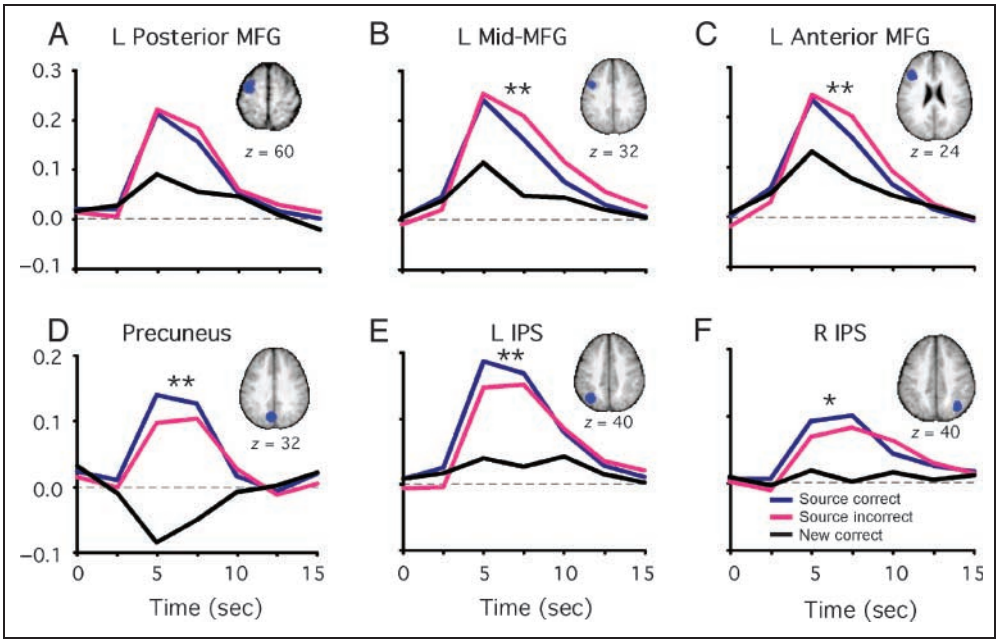


**Figure 3.** Frontal and parietal ROIs and associated time courses from the source accuracy analysis. Regions include (A) left posterior MFG near BA 6, (B) mid-MFG near BA 9, (C) anterior MFG near BA 46, (D) precuneus near BA 7, (E) left IPS near BA 40, and (F) right IPS near BA 40. Four of the ROIs appear in Figure 2. Time courses begin at stimulus onset, denoted by time zero. Dashed lines at zero signal change reflect baseline. Units are in percent signal change from baseline. Horizontal slice atlas coordinates are listed below each ROI image.

differences between correct and incorrect source trials were significant in both regions, mid-MFG, $t(25) = -2.38$, $p < .05$, and anterior MFG, $t(25) = -2.75$, $p < .05$.

In contrast, the three parietal ROIs were more active on source correct than on source incorrect trials. The difference was significant at time points 5.0 and 7.5 sec in precuneus and left IPS and marginally significant in the right IPS; precuneus, $t(25) = 2.18$, $p < .05$, two-tailed; L IPS, $t(25) = 2.21$, $p < .05$; R IPS, $t(25) = 1.99$, $p = .06$ (Figure 3D–F). No parietal ROI differed as a function of targetness when correct old targets were compared with correct old nontargets; precuneus, $t(25) = -0.53$; L IPS, $t(25) = 0.09$; R IPS, $t(25) = -0.42$, all $p > .60$ (Figure 2, right panels).

We tested whether the two MFG ROIs with significant source accuracy effects (mid-middle frontal gyrus and anterior MFG) differed reliably from parietal ROIs. The peak BOLD responses in the two MFG ROIs and the three parietal ROIs were averaged separately. This procedure created an MFG and a parietal signal average for correct and incorrect source trials (Figure 4). We then entered the averaged data into a 2 × 2 ANOVA, with location (MFG and parietal) and accuracy (source correct and source incorrect) as fixed factors and subject as a random factor. The analysis produced a main effect of location, $F(1,25) = 17.95$, $p < .0001$, indicating that activity was greater in MFG than in parietal ROIs. Importantly, we also found a highly significant location by accuracy interaction, $F(1,25) = 40.30$, $p < .0001$, supporting the observation that MFG and parietal ROIs were differentially engaged by source accuracy. The main effect of accuracy was not significant ($p > .92$).

Due to its critical role in memory encoding and retrieval, we also examined time courses in the two ROIs located near the HG (Figure 1) and found relatively weak modulations (<0.1%) and differing patterns of response in the left and right HG. In the left HG (−23, −41, −6), modulations in signal were observed only at time point 5.0 sec (T+ = −0.01% signal change, T− = −0.06, NT+ = −0.04, NT− = −0.03, and N+ = −0.07). Despite the modest signal changes, an ANOVA with five levels of condition (T+, T−, NT+, NT−, and N+) on time point 5.0-sec signal magnitudes (% from baseline term) revealed a significant main effect of condition, $F(1,25) = 6.98$, $p < .0001$. Post hoc Tukey HSD tests revealed that only the T+ versus N+ and the T+ versus T− comparisons differed significantly ($p < .05$). In the right HG (+30, −35, −9), ANOVA revealed significant effect of condition, $F(1,25) = 3.30$, $p <$

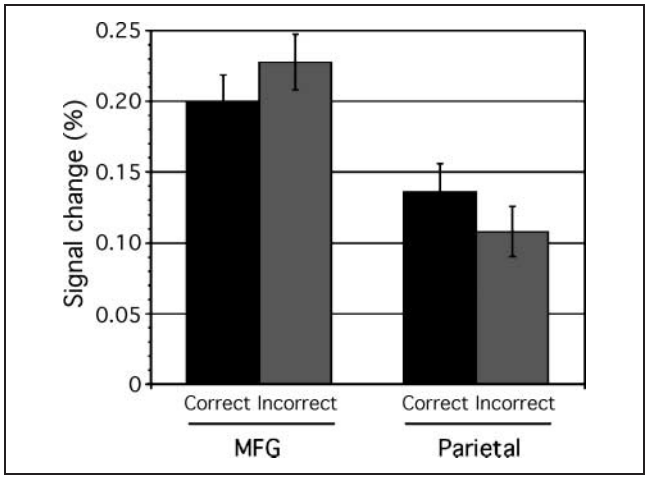


**Figure 4.** Average peak signal change values from the two MFG and three parietal ROIs, displayed in Figure 3, for source correct and incorrect trials. Error bars reflect *SEM*. Note that the MFG average includes posterior MFG, a region in which activity differences between correct and incorrect source trials did not reach significance.

.05, but only the NT− versus NT+ comparison differed using the Tukey HSD method.

### Retrieval Success Regions Signal Success and Error

The preceding analyses support a number of conclusion: (1) We replicated the finding that a set of frontal and parietal brain regions is modulated as a function of retrieval success; (2) we replicated previous findings that parietal regions are not modulated by the status of test items as targets and extended this finding to include the entire set of retrieval success regions; and (3) we demonstrated a novel dissociation between frontal and parietal retrieval success regions, based on the finding that left frontal retrieval success regions were more active on incorrect than correct source judgments, whereas medial and lateral parietal regions were more active on correct than incorrect source judgments. To further evaluate the functions of the retrieval success regions, we conducted additional exploratory analyses to more carefully examine the pattern of activity across the retrieval success network. We extracted the time course of BOLD response for all five conditions from each ROI. This process led to the formation of two broad characterizations of the function of a subset of the retrieval success regions (Figure 5).

Notably, precuneus and IPS were most active when old items were judged old (T+, NT+, and NT− trials), least active when new items were judged new (N+ trials), and intermediate when there was the possibility of a mixture of old and new judgments to old items (T− trials). In addition, T− trials were associated with an intermediate response (Figure 5A), with the right and left IPS patterns being similar (right IPS not shown). To test the reliability of the observed differences, we compared BOLD responses across precuneus, left IPS, and right IPS by first computing a one-way ANOVA with five levels of response category (T+, T−, NT+, NT−, and N+) on the estimated peak data from each ROI. This analysis identified a significant main effect of response category in each ROI; precuneus, $F(1,25) = 35.49$, $p < .0001$; left IPS, $F(1,25) = 28.42$, $p < .0001$; right IPS, $F(1,25) = 10.68$, $p < .0001$. Pairwise comparisons (using Tukey HSD) confirmed that the observed differences in activity (T+ = NT+ = NT− > T− > N+) were statistically significant ($p < .05$; see Figure 5A). The one exception was activity in the right IPS on T− trials, which did not differ significantly from T+ and NT+ trials.

In contrast, regions in AI/FO and dACC/medial frontal gyrus (meFG) showed a pattern of activity that was similar to the MFG regions. In AI/FO and dACC/meFG, activity increased the most on incorrect source judgments, the least for correct new items, and was intermediate for correct source judgments (Figure 5B). To test the significance of the effects, we computed a one-way ANOVA on the estimated peak BOLD responses in the right and left AI/FO and dACC/meFG, with category of response as the only factor. This set of analyses revealed significant differences among categories in all three ROIs; right AI/FO, $F(1,25) = 33.29$, $p < .0001$; left AI/FO, $F(1,25) = 23.68$, $p < .0001$; dACC/meFG, $F(1,25) = 18.78$, $p < .0001$. Post hoc comparisons using the Tukey HSD ($p < .05$) method indicated a difference in activity between

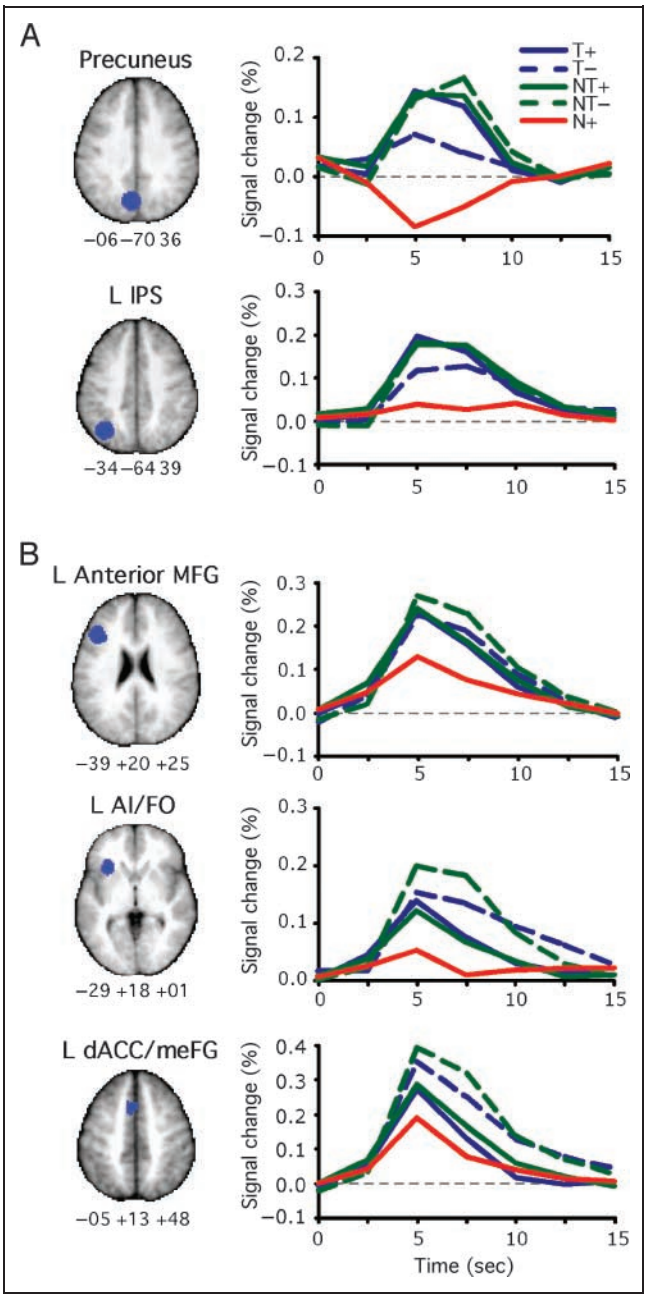


**Figure 5.** Regions of interest from the exploratory analysis are projected over horizontal slices of the average anatomic image. Timecourses of BOLD responses for correct (solid) and incorrect (dashed) items are displayed. Regions include (A) precuneus and left intraparietal sulcus (L IPS) and (B) left anterior middle frontal gyrus (L anterior MFG), left anterior insula (L AI/FO), and doral anterior cingulate/medial frontal gyrus (dACC/meFG). Peak atlas coordinates ($x$, $y$, $z$) are displayed below the ROI images. Horizontal slices were located near the $z$ atlas coordinate for each ROI.

incorrect and correct old trials in the right AI/FO and dACC/meFG (Figure 5E and F). In the left AI/FO, the pattern of responses was similar but the difference between T− and T+ failed to reach significance after correction for multiple comparisons (Figure 5B, middle panel). Overall, AI/FO and dACC/meFG were most active when old items were given an incorrect response and least active on N+ trials.

As indicated by the RT analysis reported earlier, error trials were associated with significantly longer RTs than correct trials. This raises the possibility that AI/FO and dACC/meFG activities correlated with RT. To explore this possibility, we computed a regression analysis for the frontal and parietal ROIs using the mean RT and the estimated peak signal change (time points 5.0 and 7.5 sec) for each subject. This analysis revealed a significant correlation between RT and signal change (%) in the left AI/FO ($R^2 = .12$), $F(1,118) = 15.65$, $p < .0001$, and right AI/FO ($R^2 = .04$), $F(1,118) = 5.00$, $p < .05$, but not in dACC/meFG ($R^2 = .02$), $F(1,118) = 1.91$. Regression analysis in the three MFG and three parietal ROIs showed no relationship between signal change and RT (all $p > .09$). When trial type was included as a covariate in the model, the correlation in the left AI/FO was marginally significant ($p = .08$), but no other ROIs approached significance. Thus, the pattern of response magnitudes in AI/FO tended to track with RT, increasing most at time points 5.0 and 7.5 sec on trials with the longest mean RT and the least on trials with the shortest mean RT. We note, however, that the effect size was small, indicating that other sources of variance were left unexplained by the RT analysis.

## DISCUSSION

Brain imaging studies of retrieval success have consistently revealed a set of regions (including frontal and parietal cortices) that have not historically been associated with episodic memory processes. The present study examined the functional significance of these retrieval success regions using a source memory task and event-related fMRI. Source memory tasks provide one of the strongest means of operationally defining episodic retrieval because, in theory, the requirement to "remember the source" necessitates that subjects recollect contextual information about personal study episodes. We found that parietal retrieval success regions exhibited a graded "oldness" response; a larger transient response for old items receiving correct source judgments than for those responded to incorrectly (relative to a baseline response provided by correctly rejected new items). That is, the magnitude of the response correlated with subjects' ability to retrieve source information (Figures 3 and 5). In contrast, a set of frontal regions exhibited an error-related response, such that activity increased the most on error trials (which have the longest RTs; Figures 3 and 5). Subsequently we discuss possible functions performed by retrieval success regions and offer an accumulator model to account for the pattern of activity observed across the network.

### None of the Retrieval Success Regions Are Modulated by Target Status

Although they were sensitive to the accuracy of source memory, regions exhibiting retrieval success effects (Figure 1) were not selectively sensitive to the retrieval of "target" items per se; old target and nontarget items exhibited equivalent responses. This is important because one interpretation of findings from studies of item recognition is that retrieval success effects simply emphasize identification of a particular type of stimulus (i.e., the old stimuli are "targets" during item recognition), independently of retrieval. One advantage of our experimental design was that it allowed us to compare source retrieval and targetness simultaneously, firmly ruling out an explanation in terms of targetness. Instead our results extend those of Shannon and Buckner (2004), in which parietal regions where shown to exhibit retrieval success effects regardless of whether subjects were instructed to respond only to old, new, or both old and new items. The current data demonstrate that this behavior is not unique to parietal cortex, confirming that the entire set of regions that produce old/new retrieval success effects respond regardless of the target status of old stimuli.

We highlight one potential complication in finding that target status does not modulate retrieval success regions; the failure to find effects in this kind of analysis could in part reflect the composite nature of the conditions. For example, based on electrophysiological evidence Herron and Rugg (2003; see also Rugg et al., 2003) noted that, during source memory tasks, correct responses to nontargets could consist entirely of correctly recollected old items, or could reflect items that are not recollected at all because participants are able to successfully orient toward target information only, or some mixture of the two strategies. Similarly, in theory, responses to nontargets could be made based on familiarity in the absence of recollection (as per Jacoby's, 1991, original characterization) or even on the basis of forgetting (where participants genuinely believe the nontarget items are new). Thus, although the source memory paradigm provides a very strong operational definition of episodic recollection per se, no single task can rule out individual differences in memory. While we do not believe that this renders the present findings any less compelling and behavioral evidence rules out some possibilities (e.g., forgetting seems unlikely to play a large role in the current study), further studies that separate individual differences in retrieval strategy may be useful.

Taken together, the evidence suggests that retrieval success regions in both frontal and parietal cortices track the recovery of information from episodic memory independent of task demands that direct the remember toward a particular type of information. Note, however, that

this conclusion does not rule out other influential factors. For example, the probability manipulation by Herron et al. (2004) influenced the retrieval success effect in some areas (notably superior parietal cortex; close, but not identical to, the common more lateral and ventral posterior parietal retrieval success areas) but not in others. Quite why stimulus probability plays such an important role for superior parietal cortex remains unclear at present. What is clear, however, is that the retrieval success regions are consistently found to be sensitive to episodic memory across a range of studies, and any attempt to characterize their functional role must now account for a number of empirical findings provided by fMRI.

### Source Retrieval Errors

Relative to correct source judgments (T+ and NT+), errors in source retrieval (T− and NT−) were associated with increased activity in lateral and medial regions of frontal cortex. Our findings are consistent with a number of studies that associate frontal activity with strategic processing during episodic retrieval and working memory (Kahn et al., 2004; Ranganath, 2004; Buckner, 2003; Velanova et al., 2003; Dobbins et al., 2002; Rugg et al., 2002; Buckner & Wheeler, 2001; Donaldson, Petersen, & Buckner, 2001; Donaldson, Petersen, Ollinger, et al., 2001; Ranganath, Johnson, & D'Esposito, 2000; Buckner, Koutstaal, Schacter, Dale, et al., 1998; Buckner, Koutstaal, Schacter, Wagner, & Rosen, 1998; Cabeza et al., 1997). The heightened response on error trials suggests that retrieval monitoring occurs in a distributed set of regions, including dACC, MFG, and AI/FO. Later we consider two functional accounts of the activity seen in the present study during error trials.

Studies of response uncertainty and decision making have implicated AI/FO and medial frontal cortex, including cortex spanning dACC and medial frontal gyrus (Thielscher & Pessoa, 2007; Fleck, Daselaar, Dobbins, & Cabeza, 2006; Grinband, Hirsch, & Ferrera, 2006; Huettel, Song, & McCarthy, 2005; Critchley, Mathias, & Dolan, 2001). For example, in a recent fMRI study of perceptual decision making, Ploran et al. (2007) examined timing-dependent perceptual recognition responses and found that the onset of activity in AI/FO and medial frontal areas occurred at the time of, or just after, decisions about object identity. This late response occurred even when recognition was incorrect (Wheeler, Petersen, Nelson, Ploran, & Velanova, 2008). In the task, drawings of objects were revealed gradually over 16 sec from under a white noise mask until they were fully revealed. Subjects noted the timing of recognition by pressing a button then noted their accuracy by pressing it again when the object was fully revealed. The revelation task produced a significant variability in the timing of recognition, which allowed examination of the temporal profile of the evolving BOLD signal in the period leading up to, during, and after perceptual recognition. The present findings in AI/FO and dACC are consistent with a role in decision making (i.e., performance monitoring) because of the increased activity on error trials.

Dosenbach, Fair, Cohen, Schlaggar, and Petersen (2008) and Dosenbach et al. (2006, 2007) have introduced a more specific formulation for the function of AI/FO and medial frontal areas. They performed a meta-analysis on 10 imaging studies ($n$ = 183) that used a mixed block/event-related approach across a range of cognitive tasks (Dosenbach et al., 2006). Among other findings, they identified a small set of "core" task-set regions that displayed (1) transient responses related to task onset, (2) sustained activity throughout (but not between) task blocks, and (3) robust error-related responses. The proposed function of task set regions is to interpret and to maintain over time task instructions that configure and monitor trial-related processes. This core set consisted exclusively of AI/FO and dACC/meFG. Interpreted from within the task-set framework, heightened AI/FO and dACC/meFG activity on error trials in the present study could be related to an increased need for control during uncertainty or for feedback processing related to performance monitoring.

Although no external feedback was provided in the current study, error trials can be associated with a corrective response in which the initial (erroneous) response is later deemed to be incorrect. Thus, the increase in activity could have been due to internally generated error awareness. Or the increase in activity could have been related to other sources such as a general level of increased uncertainty, having pressed the wrong button by accident, or to increased attentional demands. At present, we cannot dissociate among these alternatives.

### Parietal Activity Was Associated with Old/New Evidence

We found that precuneus and anterior IPS were most active for items judged to be old and least active for items judged to be new (Figure 5A). We also observed an intermediate level of activity in the T− condition, which was most likely associated with a mixture of old (large signal change) and new (small signal change) judgments. This pattern of activity is consistent with prior reports indicating that some regions of parietal cortex modulate according to the outcome of the old/new decision, independently of accuracy. For example, Kahn et al. (2004) and Wheeler and Buckner (2003) have both reported that left IPS was more active for items judged to be old than items judged to be new, regardless of whether they were actually old or new (see Wagner et al., 2005). Thus, by this view, activity in IPS and precuneus tracks the outcome of the old/new decision rather than the true item status.

Interestingly, the perceptual decision-making study by Ploran et al. (2007; Wheeler et al., 2008) identified a left parietal region, located in or near the IPS, in which activity accumulated before the moment of recognition at a rate that correlated positively with recognition timing. That is, when recognition occurred early, activity in IPS

(and in 10 other regions) increased rapidly after onset. However, when recognition occurred later in the revelation process, activity increased significantly more slowly, a neural accumulation process that may be functionally related to the pattern of "old" > "new" decision-related activity we have observed in the present study. One problem with this comparison, however, is that in the current study, no significant correlation was found between the size of activity and the behavioral RTs. There are of course considerable differences between the two studies that could have functional consequences; Ploran et al. used a slow reveal procedure designed to tease apart differences based on recognition timing, and only new items were present with no source or target task demands. Moreover, the additional monitoring and control processes demanded by memory tasks (compared with perceptual tasks) may inherently reduce the correlation between accumulated evidence and overt behavior. In either case, it will be of considerable interest to discover whether equivalent correlations with RT are evident within these regions in memory studies that are designed with this purpose in mind.

### An Accumulation Model of Mnemonic Decisions

Here we present a conceptual model that relates the patterns of frontal and parietal neural activity to processes underlying episodic memory decisions. Our view is derived from detailed examination of the different roles that these regions appear to play in the current study, which suggests an accumulation of evidence toward memory decisions for parietal regions and a role in decision processes for frontal regions. The concepts are derived from accumulator models of memory and decision making (Usher & McClelland, 2001; Ratcliff & McKoon, 1982; Ratcliff, 1978). Similar models have recently been used to account for neural responses to motion detection in Macaque IPS (Gold & Shadlen, 2007; Shadlen, Britten, Newsome, & Movshon, 1996; Shadlen & Newsome, 1996) and Dorsolateral Prefrontal Cortex (Kim & Shadlen, 1999) as well as in motor cortex during initiation of motor behavior (Hanes & Schall, 1996) and superior colliculus during distance discrimination (Ratcliff, Cherian, & Segraves 2003). Our model (Figure 6) consists of four levels of processing, including an early stage of stimulus analysis and a final stage of response generation. Stimulus analysis is not limited to sensory processing, as it would include mnemonic information possibly supplied by MTL structures. Between stimulus input and response output, decisions are formed based on accumulated evidence about the mnemonic status of items relative to a criterion parameter (derived from task instructions and other motivational factors).

On the basis of our data, we propose that evidence accumulation for old and new information occurs (at least in part) in parietal retrieval success regions. By this view, the level of BOLD signal change in these regions reflects the on-line accumulation of information about the stimulus that is relevant to the task judgment, and the amount of activity directly reflects the current balance of evidence in favor of a goal-directed response. For example, evidence accumulation could be related to degree of temporal context,

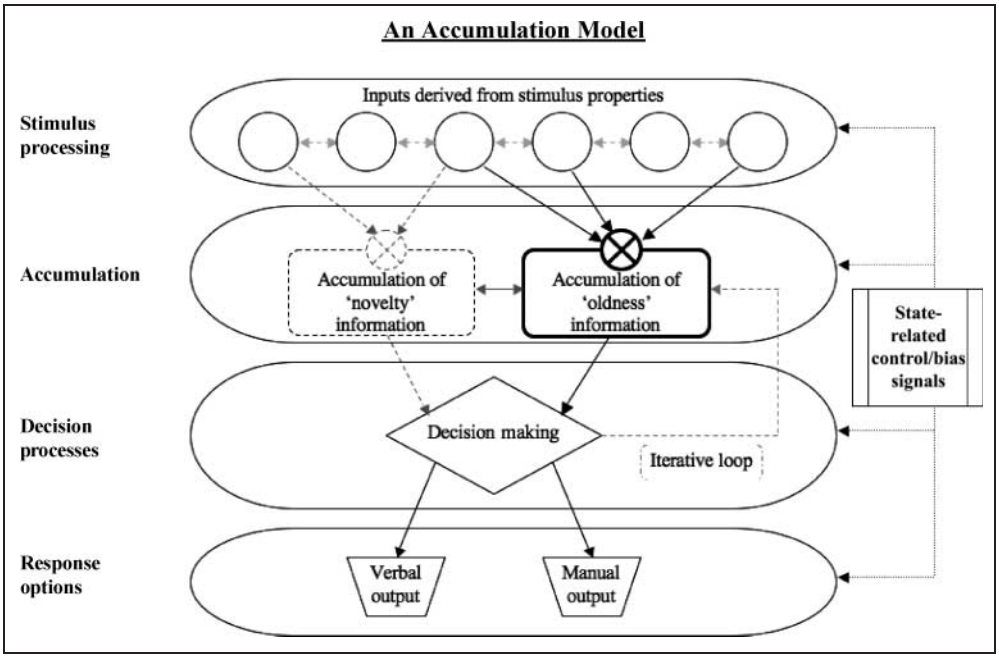


**Figure 6.** An accumulation model for parietal activity in old/new decisions. Different levels of processing are depicted, from stimulus processing to response output. Each of the levels depicted is intended to reflect a cortical region (or set of regions), and as such the interactions between regions are likely to be bidirectional (allowing feed-forward and feedback mechanisms to operate). State-related control or bias signals are also highlighted, which could potentially operate at each level of the system to modulate behavior depending on the current task context (e.g., gating which input variables are relevant, biasing outputs toward a particular response, etc.). Alternative formulations of the model are plausible given currently available data (e.g., a single accumulator that is flexibly sensitive to different types of information) and some aspects of the model are difficult to test with fMRI (e.g., on-line iterations between decision making and accumulation). The "accumulation of oldness" component is shown in bold, highlighting the correspondence with the posterior parietal "retrieval success" regions investigated in the present study.

level of familiarity, or recollected detail accompanying a particular memory. Importantly, by "goal directed," we do not simply mean the amount of prior exposure per se; rather, we assume that this evidence is context dependent and task relevant.

Viewing the anterior IPS and precuneus regions in terms of an accumulation model has several implications. First, the neural counter must receive inputs (property or feature information) from earlier stages of the processing chain. A large number of regions (including hippocampus and related medial-temporal structures) could be involved, reflecting different aspects of the processing of a stimulus. It also seems likely that different sets of regions could provide an input depending on the particular type of stimulus being processed (e.g., verbal vs. nonverbal). Second, if evidence is only meaningful in the context of a given task, mechanisms must exist to delineate what variables (stimulus properties) are considered relevant. This is likely to be dependent on both the particular properties currently available and the application of top–down state-related "control" or "biasing" signals. Such strategic control can influence neuronal processing at many levels by biasing activity (Miller & Cohen, 2001; Desimone & Duncan, 1995; Posner & Petersen, 1990) and may be evident as state-related modulations of activity seen in fMRI studies of memory (Velanova et al., 2003; Donaldson, Petersen, Ollinger, et al., 2001). Third, the counter must, in turn, provide an output that is available to later stages of the processing chain, allowing generation of an overt response. Such decision-making processes presumably either read the current count directly (e.g., comparing it to a threshold) or use the count as one of many contributing factors in a decision. One key aspect of decision processing is clearly the detection of errors, and evidence suggests that frontal retrieval success regions are likely to play a role in the overall decision process (see Dosenbach et al., 2006, 2008; Wheeler et al., 2008; Ploran et al., 2007). Furthermore, because decision processes can clearly be adapted in real time, we note that the counter must be adjustable on a trial-by-trial basis (Logan & Gordon, 2001).

One reason for making this model explicit is to raise questions and to produce testable hypotheses. For example, can state-related control processes influence all or just some levels of the system, from gating which stimulus properties are relevant to biasing the decision making toward a particular response? Which stages of processing correlate with measures of overt behavior (e.g., RTs), and do some operations specifically interrupt or interfere with this relationship? Would a parietal accumulation mechanism (whether related to RT or not) generalize to other tasks or is it specialized for old/new decisions? To what extent is it consistent with outcomes predicted by recent attentional accounts? The model also highlights aspects of retrieval that are extremely difficult to examine with fMRI because of the low temporal resolution of the data. For example, the rapid on-line operation of this system is likely to involve multiple iterative interactions between lower level feature detection/counters and higher level control and decision-making processes.

Here we consider one potential problem for our model. If no neural evidence is accumulating for new items, how is a response generated? One explanation can be ruled out; a time-out mechanism is not in operation. If it were, correct rejection responses would take longer than source recognition responses when in fact they are typically quicker. We offer two speculative explanations. First, a minimum threshold, which when combined with an iterative decision-making process, allows stimuli producing no "counts" to be rejected relatively quickly. Second, a separate novelty detection system, either as a first stage (serially) that allow new items to be rejected before "oldness" is assessed, or as an alternative counter (in parallel) that contributes information to the broader decision-making process (as depicted in Figure 6). Future studies identifying how sources of evidence contribute to decision outcome should help distinguish between these competing possibilities.

Finally, we note that the accumulation model could be viewed as a mechanism that exclusively supports recollection. Equally, however, it may reflect a central memory index, providing information that supports evidence derived from familiarity and recollection, with the distinction between these processes depending on the type of information being retrieved, the current task context, and/or the employment of postretrieval monitoring and control processes (for a similar view based on behavioral data, see Leboe & Whittlesea, 2002). Regardless, one reason for proposing the model is that it need not necessarily map directly onto familiarity or recollection. To our minds, it seems unlikely that indices of memory retrieval provided by fMRI will fit exactly with the traditional discrete memory constructs, particularly when the distributed multicomponent nature of brain processing is taken into account.


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