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# An investigation of the effects of relative probability of old and new test items on the neural correlates of successful and unsuccessful

# source memory

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# Abstract

The present event-related fMRI study addressed the question whether retrieval-related neural activity in lateral parietal cortex is affected by the relative probability of test items. We varied the proportion of old to new items across two test blocks, with 25% of the items being old in one block and 75% being old in the other. Prior to each block, participants (N=18) completed one of two types of study judgment on each of 108 object images. They then performed a source memory test with four response options: studied in task 1, studied in task 2, old but unsure of the study task, and new. Retrievalrelated activity in regions previously identified as recollection-sensitive, including the left inferior lateral parietal cortex and bilateral medial temporal cortex, was unaffected by old/new ratio. Generic retrieval success effects - retrieval-related effects common to recognized items attracting either a correct or an incorrect source judgment - were identified in several regions of left superior parietal cortex. These effects dissociated between a middle region of the intraparietal sulcus (IPS), where activity did not interact with ratio, and regions anterior and posterior to the middle IPS where activity was sensitive to old/new ratio. The findings are inconsistent with prior proposals that retrieval-related activity in and around the left middle IPS reflects the relative salience of old and new test items. Rather, they suggest that, as in the case of more inferior left parietal regions, retrieval-related activity in this region reflects processes directly linked to retrieval.

# Keywords

episodic memory; recognition memory; remember-know; event-related potential; episodic buffer

Functional neuroimaging studies have identified several cortical regions where neural activity is enhanced for successful recognition memory judgments relative to correct rejection of new test items (for reviews see Wagner et al., 2005; Skinner & Fernandez, 2007; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008a; Rugg and Henson, 2002). Activity in a number of these regions, notably lateral parietal and frontal cortex, appears to dissociate according to whether recognition is based on an acontextual sense of prior occurrence (familiarity) or is accompanied by retrieval of qualitative information about the study episode (recollection; e.g., Yonelinas et al., 2005; Wheeler & Buckner, 2004; Daselaar, Fleck, & Cabeza, 2006; Montaldi

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et al., 2006; Vilberg & Rugg, 2007). More specifically, retrieval-related activity in left lateral inferior parietal cortex and left superior prefrontal cortex has been linked to recollection, whereas activity in left superior parietal cortex and left anterior/lateral prefrontal cortex has been associated with familiarity-driven recognition (see e.g., Yonelinas et al., 2005; Vilberg & Rugg, 2007).

We have proposed (Vilberg & Rugg, 2008a; 2008b) that left lateral inferior parietal cortex supports the representation or maintenance of retrieved episodic information. By contrast, we have argued that the more superior left parietal region, which includes the middle (horizontal) segment of the left intraparietal sulcus, is responsive not to familiarity, or even to retrieval success *per se*, but rather to the relative salience of retrieval cues associated with different memory outcomes. By this argument, the greater activity elicited by items judged old rather than new reflects the fact that, under most circumstances, old items are treated as 'targets' to be detected against a background of less relevant 'non-targets' (new items). Thus the enhanced left superior parietal activity elicited by old items reflects their target rather than their mnemonic status. These proposals have not gone unchallenged. Notably, it has been argued that the dissociation between retrieval-related activity in superior and inferior left lateral parietal cortex reflects the roles played by these regions in 'top-down' versus 'bottom-up' attention respectively (Ciaramelli, Grady, & Moscovitch, 2008; Cabeza, 2008; Cabeza et al., 2008).

To elucidate the functional roles of regions demonstrating 'retrieval success effects' such as those described above, manipulations that selectively affect the different processes active during a retrieval attempt are needed. Herron, Henson, and Rugg (2004) utilized this logic in an effort to dissociate regions acting *downstream* of retrieval from regions directly involved in the act of retrieval itself. They investigated the effects of varying the relative probability of 'old' and 'new' recognition test items, arguing that regions that participate directly in retrieval should be unaffected by this manipulation. Because neural activity can only vary according to the relative probability of old and new items after the items have been identified as such, they further argued that regions where activity varies with old/new ratio are likely linked to processes downstream of, or contingent upon, the retrieval attempt. Herron, Henson, and Rugg identified one set of regions, including left inferior and medial parietal cortex, where retrieval success effects were probability-insensitive, and another set, which included left prefrontal and left superior parietal cortex, where retrieval success effects varied according to old/new probability. In most of these latter regions, the effects varied in direction according to whether old or new items were the rarer stimulus class, with the more infrequent items eliciting greater activity. Following the logic outlined above, these regions are unlikely to directly support the recovery or representation of stored information. Accordingly, Herron, Henson, and Rugg characterized these regions as reflecting processes downstream of retrieval.

A major limitation of the study of Herron, Henson, and Rugg (2004) arises from the failure to use a test procedure that allowed segregation of test items recognized on the basis of familiarity vs. recollection. Thus, it was not possible to determine the extent to which probability-sensitive and probability-insensitive retrieval effects overlapped regions where activity also dissociated according to the nature of the information supporting the recognition decision. The present study attempted to redress this weakness in the prior study by investigating the effects of old/ new ratio on the neural correlates of successful versus unsuccessful source memory. A primary aim was to determine whether the neural correlates of successful recollection (as operationalized by successful source memory) are sensitive to the relative frequency with which recollection occurs. Were this to be the case, it would seriously undermine the proposal that recollection-related retrieval effects in left inferior parietal cortex identify regions that support the recovery and maintenance of recollected information (see Vilberg & Rugg, 2008a). Such a finding would instead offer support for the alternative proposal that inferior

parietal recollection effects reflect the bottom-up reorienting or 'capture' of attention (Ciaramelli, Grady, & Moscovitch, 2008, Cabeza, 2008; Cabeza et al., 2008), since these processes are held to be probability-sensitive (Corbetta, Patul, & Shulman, 2008).

# **Materials and Methods**

#### Subjects

Subjects were right-handed, native English speakers aged between 18 and 26. A total of 23 individuals (14 female) took part in the experiment. In accordance with the requirements of the UCI Institutional Review Board, which approved the study, all subjects gave informed consent prior to participating. Five subjects were excluded from all analyses due to inadequate behavioral performance (correct rejection accuracy < 50%).

#### Stimuli

Stimuli were color photographs of objects superimposed on a black background. The pool of object images used to create stimulus lists comprised 752 pictures drawn from the Amsterdam Library of Object Images (ALOI) (Geusebroek, Burghouts, & Smeulders, 2005). Allocation of object images to experimental conditions was randomized on a subject-specific basis. For each subject, 216 images were selected to be presented at study, 108 in each of two study blocks. An additional 144 images were selected to serve as new test stimuli, 108 in the low old-item probability block and 36 in the high old-item probability block. Twelve other images were selected from the stimulus pool to be used in a short practice session, and another ten images were used as buffers in the study and test blocks.

Object images were presented individually at study, each within a white frame located either in the left or right half of the display. An equal number of images were chosen randomly to be displayed to the left or right of center for each subject. Object images subtended up to 5.57 degrees of visual angle, while the white frame surrounding object images subtended 7.94 degrees of visual angle (vertical and horizontal). In the low old-item probability test block (hereafter referred to as the 'low ratio' block), 36 of the 108 studied images were presented at test, whereas in the high old-item probability test block (hereafter referred to as the 'high ratio' block), all 108 of the previously studied images were presented at test. Old items in each block were sampled equally from the two possible study locations. Two buffer trials were added to the beginning and end of each study list, and three buffer trials were added to the beginning of each test list.

## Procedure

Subjects completed a short practice session outside of the scanner prior to beginning the first study session. The practice session consisted of one study and one test practice block of 8 and 12 trials, respectively. Subjects received instructions on how to perform both tasks prior to beginning the study practice. After practice, participants were informed that they would undergo two study-test cycles, and that the proportion of old and new items in each block would differ. Specifically, they were informed that in one block there would be relatively more new than old items, and that in the other there would be relatively more old than new items. Participants were not instructed as to which block would occur first. They were instructed to respond to each stimulus on the basis of their memory for that stimulus, rather than to use the apparent old/new ratio to guess whether each test cue was old or new. Participants were then positioned in the scanner and remained there for the duration of the two study-test cycles.

Study trials consisted of the presentation of a central fixation cross for 500 ms, followed by a task cue for 1000 ms, then an object image for 1000 ms, a centrally-located question mark for 2000 ms, and a blank screen for 500 ms. On half of the study trials, a hard/soft task cue was

presented, and on the other half, a big/small task cue was presented, with the assignment of object images to task cues performed randomly on a subject-specific basis. The hard/soft task cue was composed of the words "Hard/Soft" centered above a white arrow pointing toward a white frame located in the left hemisphere of the display. The big/small task cue was composed of the words "Big/Small" centered above a white arrow pointing toward a white frame located in the right hemisphere of the display. The white frame remained in the same position on the screen after the task cue display ended, framing the object image in that same side of the screen. Both the arrow and the cue instruction (i.e., "Hard/Soft" or "Big/Small") also remained on the screen during stimulus presentation. The study task to be performed in conjunction with the Hard/Soft cue was to decide if each object, in real life, would compress if squeezed. Thus, a hard response corresponded to an item believed to not give under pressure whereas a soft response corresponded to an item believed to give under pressure. The study task to be performed in conjunction with the Big/Small cue was to decide whether the object displayed would, in real life, be larger or smaller than a shoebox. Participants used the index fingers of each hand to indicate their responses, with Hard or Big corresponding to the left index finger and Soft or Small corresponding to the right. After completing each of the two study sessions, participants were given a 5 minute break during which test instructions were read by the experimenter to the participant over headphones.

The two test blocks differed in the proportion of old and new items present in each list. Each participant was pseudo-randomly assigned an ordering of the two test lists such that across all participants, half would receive the high ratio list first. In each test block, old and new items were randomly interspersed with 36 null events. All test trials began with a red fixation cross for 500 ms followed by an object image in a white frame for 500 ms, followed by a white fixation cross for 2600 ms. In the case of null events, the red fixation cross was followed directly by a white fixation cross which remained on the screen for 3100 ms. All test stimuli were presented in central vision. A source memory test was employed. Four responses were possible: new, old studied with hard/soft task (or old studied to the left of center), old studied with big/ small task (or old studied to the right of center), and old but don't remember the study task. Participants were instructed to use the source responses (old studied with hard/soft, old studied with big/small) only when confident of the study task (or location), and to use the 'don't remember' response only when confident an item had been studied. The New key was to be used when participants judged that a test picture was new or when they were uncertain whether the test picture was old.

Participants were instructed to use the index, middle, and ring fingers of one hand to make source-specifying responses and source uncertain responses, respectively, and the index finger of the other hand to respond New. Hand assignment was randomized across subjects. Two keypads were used to make responses in the scanner. A five minute break was given between the end of the first test session and the start of the second study session.

#### fMRI Data Acquisition

High-resolution T1-weighted anatomical images ( $240 \times 240$  matrix, 1 mm<sup>3</sup> voxels) and blood oxygenation level-dependent (BOLD), T2\*-weighted echoplanar functional images (SENSE factor of 1.8, flip angle 70°, 80 × 80 matrix, FOV = 24 cm, TR = 2000 ms, TE = 30 ms) were acquired using a 3T Philips Achieva MRI scanner equipped with an 8 channel receiver head coil (Philips Medical Systems, Andover, MA). Three-hundred and forty-one volumes were acquired during each test session. Each volume comprised 30 slices oriented parallel to the AC-PC line (thickness 3mm, 1mm inter-slice gap, 3mm<sup>3</sup> voxels) acquired in an ascending sequence. The first 5 volumes of each session were discarded to allow equilibration of tissue magnetization.

#### fMRI Data Analysis

Statistical Parametric Mapping (SPM5, Wellcome Department of Imaging Neuroscience, London, UK), run under Matlab R2006a (The Mathworks Inc., USA) was used for fMRI data analysis. Functional imaging timeseries were subjected to realignment (to the first retained volume), reorientation, spatial normalization to a standard EPI template (based on the Montreal Neurological Institute (MNI) reference brain; Cocosco et al., 1997) and smoothing with an 8mm FWHM Gaussian kernel. Analysis was performed using a General Linear Model (GLM) in which a delta function was used to model neural activity at stimulus onset. These functions were convolved with the canonical hemodynamic response function (HRF) and its temporal and dispersion derivatives to model the BOLD response (Friston et al., 1998). The analyses of the parameter estimates of the temporal and dispersion derivatives added little to the findings obtained with the canonical HRF, and therefore are not reported. For each test block, five eventtypes (source correct hits [SC], source incorrect and source guess item hits [SI], Misses [M], correct rejections [CR], along with events of no interest such as buffer trials, and trials with incorrect or omitted responses) were modeled. For each block, the model also included as covariates the across-scan mean and six regressors representing motion-related variance (three for rigid-body translation and three for rotation). For one of the subjects, one scan associated with > 0.5 mm of translation was visibly identified, and an additional covariate modeling this scan was included. For each voxel, the image time-series was high-pass filtered to 1/128 Hz and scaled to create a grand mean of 100 across voxels and scans. An AR(1) model was used to estimate and correct for non-sphericity of the error covariance (Friston et al., 2002). The GLM was used to obtain parameter estimates representing the activity elicited by the events of interest.

A statistical threshold of p < 0.001, uncorrected, with an extent threshold of 5 contiguous voxels was employed for the principal unidirectional contrasts. A threshold of p < 0.002 was used for bidirectional (F) contrasts so as to yield one-tailed p-values of 0.001. F contrasts employed as exclusive masks were thresholded at p < 0.1 to produce one-tailed mask p-values of 0.05 (note that the more liberal the threshold of an exclusive mask, the more conservative is the masking procedure). A small volume correction procedure based on Gaussian random field theory was used when applicable. This procedure employed a 5 mm radius sphere centered on the peak coordinates of the reference effect. A representative subject's normalized anatomical image was used to display findings on brain sections. All coordinates are reported in MNI space. Localization of effects was accomplished by visual inspection on a representative subject's anatomical image with reference to the Anatomy Toolbox v1.5 (Eickhoff et al., 2005; 2006; 2007) and the MSU utility in SPM5 (http://www.fil.ion.ucl.ac.uk/spm/ext/#MSU).

# Results

fMRI analyses were restricted to trials associated with test items correctly endorsed as old or new (i.e., recognized old items attracting correct source judgments (SC items), and incorrect or unsure judgments (SI items), along with correctly rejected new items (CR items)). Behavioral results are reported only for those participants who were included in the fMRI analyses.

#### **Behavioral performance**

Mean hit rate was 81% for each test block, against correct rejection rates of 90% and 87% for the high vs. low ratio blocks, respectively (see Table 1 for a more detailed breakdown of behavioral responses). Neither recognition accuracy, as measured by the discrimination index Pr, nor response bias, as indexed by Br (Snodgrass & Corwin, 1988), significantly differed between the two blocks (Pr values of 0.71 and 0.69 for high and low ratios respectively; Br values of 0.47 and 0.36 for high and low ratios respectively). Estimates of source recollection

were corrected for guessing under the assumptions of a single high-threshold model (e.g., Park, Uncapher, & Rugg, 2008). Corrected source recollection rates did not significantly differ between the high and low ratio blocks (0.39 vs. 0.36, respectively). It should be noted, however, that the relative frequency of successful source recollection was some three times higher in the high than the low ratio block due to the relatively greater number of old test trials in that block. Thus, the probability of making a successful source judgment relative to all trials in a test block was 0.41 vs. 0.14 for the high and low ratio blocks, respectively.

Table 2 shows mean response times (RTs) broken down by trial type. An ANOVA on the SC, SI, and CR RTs for each of the high and low ratio blocks revealed no differences according to old/new ratio. There was, however, a main effect of trial type, F(1.9, 32) = 69.96. Subsequent pairwise comparisons revealed that CRs were associated with shorter RTs than both SC and SI hits, and SC hits were associated with shorter RTs than SI hits, each p < 0.05.

## fMRI findings

To allow direct comparison with the findings of Herron, Henson, and Rugg (2004), we first sought to identify regions where simple retrieval success effects were either uninfluenced by old/new ratio or interacted with this factor. For these analyses, a single Hit category was created by collapsing the SC and SI trial types. Regions where retrieval success effects were insensitive to ratio were identified by exclusively masking the Hit > CR and CR > Hit contrasts with the F contrast of the interaction between trial type (Hit vs. CR) and ratio (high vs. low). Regions where retrieval success effects interacted with the ratio manipulation were identified by the interaction contrast itself.

Next, we sought to identify recollection-sensitive regions, and subsequently, to determine whether recollection-related activity in any of these regions interacted with ratio. Under the assumption that correct source judgments would more frequently be accompanied by recollection than incorrect source judgments, we operationalized recollection-sensitivity as the outcome of the contrast between SC and SI hits. Regions sensitive to recollection where activity was insensitive to old/new ratio were identified by exclusively masking the SC > SI contrast and, separately, the SI > SC contrast, with the F contrast of the interaction between source accuracy and old/new ratio. Regions where recollection effects and old/new ratio interacted were identified by the same interaction contrast.

# Probability-insensitive retrieval success effects

Regions where activity was greater for Hits than CRs but did not interact with ratio included left and right lateral and medial parietal cortices, as well as left dorsolateral and medial prefrontal cortex (see Figure 1 and Table 3). Contrary to our proposal that retrieval-success effects in the vicinity of the left middle IPS reflect the relative salience of old and new test items, and hence are sensitive to old/new ratio (see Vilberg & Rugg, 2008a), the probability-insensitive retrieval success effect identified in the left superior parietal cortex included this region.

Regions showing probability-insensitive CR > Hit effects included bilateral medial temporal lobe (MTL) in the vicinity of the entorhinal cortex and hippocampus, posterior cingulate, and medial orbitofrontal cortex (see Figure 2 and Table 3). In the right MTL, CR > Hit effects were found in one large cluster (k = 144) centered on the hippocampus. In the left MTL, by contrast, two smaller clusters were observed: an anterior cluster in the vicinity of the entorhinal cortex, and a more posterior cluster centered on the hippocampus. As is evident from the plots of the parameter estimates shown in Figure 2, both SC and SI hits were associated with reduced activity relative to CRs in each of these regions. ANOVAs (factors of trial type and old/new ratio) performed on the peak parameter estimates from each region revealed a main effect of

trial type in each case, and follow-up comparisons confirmed the significance of CR > Hit effects separately for SC and SI trials (all p < 0.025).<sup>1</sup> In addition, SI hits were associated with reduced activity relative to SC hits in the cingulate and right MTL clusters (each p < 0.05).

#### Probability-sensitive retrieval success effects

Interactions between trial type and old/new ratio were observed in the left and right lateral and medial parietal cortex, as well as the right occipital and left prefrontal cortex (see Table 4 and Figure 3). Inspection of the peak parameter estimates from these regions revealed that the interactions primarily took the form of greater retrieval success effects when old items were more infrequent than new items.<sup>2</sup> This trend appeared to be equally evident for SC and SI trials, and was confirmed by ANOVAs contrasting the parameter estimates for the peak voxels for SC and CR trials and, separately, SI and CR trials, for each cortical region listed in Table 4 (factors of trial type and old/new ratio). Each ANOVA gave rise to a significant trial type by ratio interaction (each p < 0.05).

The above-described interaction contrast between trial type and old/new ratio identified a medial parietal cluster which extended laterally toward the posterior segment of the IPS, as well as a more anterior left parietal cluster within the ascending segment of the IPS (Figure 3: B and C; see also Table 4). The question arises whether these left parietal ratio-sensitive regions overlap with any of the ratio-sensitive regions reported by Herron, Henson, and Rugg (2004). This was the case for the anterior cluster, which survived small volume correction with reference to the peak of a probability-sensitive left anterior parietal region reported by Herron, Henson, and Rugg (2004; x = -39, y = -30, z = 54).

To address the question of whether the findings for the left superior parietal cortex demonstrate a statistically significant dissociation between probability-sensitive (anterior and posterior regions) and probability-insensitive (middle region) retrieval success effects, an ANOVA (factors of region, old/new ratio, and trial type (hit vs. correct rejection)) was performed on the peak parameter estimates for the effects identified in each region (x, y, z coordinates of -48, -27, 54; -33, -66, 48; and -15, -78, 54 for the left anterior, middle, and posterior regions, respectively; see Figure 4). The ANOVA gave rise to a main effect of trial type [F(1, 17) = 47.90, p < 0.0001], an interaction between these two factors and region [F(1.8, 30.0) = 6.40, p < 0.01. As is evident from Figure 4, old/new ratio exerted a significantly greater effect on retrieval success effects – due largely to relatively smaller old item responses in the high probability condition – in the anterior and posterior regions than it did on effects in the middle region.

#### **Recollection effects**

Two regions exhibited probability-insensitive recollection-related effects: a small area of left inferior lateral parietal/occipital cortex, and a region within the right anterior MTL (see Figure 5 and Table 5). Inspection of the peak parameter estimates for the MTL region (which is part of the right MTL cluster identified by the CR > Hit contrast) revealed a relative reduction in activity for SI hits relative to both SC hits and CRs. An ANOVA of the peak parameter estimates (factors of trial type and old/new ratio) gave rise to a main effect of trial type [F(1.3, 22.0) = 15.44, p < 0.001], and follow-up comparisons confirmed that the estimates for the three trial types differed significantly from one another (each p < 0.025). In the left inferior parietal region, SC hits elicited greater activity than both SI hits and CRs (see Figure 4). An ANOVA on the

<sup>&</sup>lt;sup>1</sup>In the case of the posterior cingulate cluster, a main effect of old/new ratio was also evident, F(1, 17) = 9.21, p < 0.01. Here, activity was greater for all trial types when old items were more frequent. <sup>2</sup>An exception to this pattern was a right occipital cluster, where activity was greater for new than old items when new items were

<sup>&</sup>lt;sup>2</sup>An exception to this pattern was a right occipital cluster, where activity was greater for new than old items when new items were relatively rare.

peak parameter estimates for this region revealed a main effect of trial type [F(2.0, 33.7) = 10.60, p < 0.001]. Follow-up comparisons confirmed the impression that the parameter estimates for SC hits not only differed from those for SI hits, but also for CRs [both p < 0.0025], whereas estimates for SI hits and CRs did not significantly differ. This 'recollection-sensitive' left inferior parietal cluster survived small volume correction centered on the peak of the left parietal 'amount-sensitive' recollection effects identified by Vilberg and Rugg (2007; MNI: x = -39, y = -81, z = 39) and Vilberg and Rugg (2008b; MNI: x = -30, y = -84, z = 39). No effects were identified by the SI > SC contrast, and nor were any regions identified by the interaction contrast.<sup>3</sup>

# Discussion

Consistent with the findings of Herron, Henson, and Rugg (2004; see also Herron, Quayle, & Rugg, 2003), the manipulation of old/new ratio did not affect measures of response bias, response time, or recognition accuracy. Critically, estimates of source accuracy also did not differ between the high and low old/new ratio test blocks. The equivalence of these behavioral indices across the two old/new ratios enabled a comparison of brain activity associated with different trial types in the absence of performance confounds. There was however a marked disparity in response time between correct rejections and recognition hits. Regardless of source accuracy, RTs to hits were on average some 400 ms slower than correct rejections (see Table 2). This pattern, which is frequently observed in studies of source memory (e.g., Rugg, Henson, Robb, 2003), suggests that subjects engaged in what Kahn, Davachi, and Wagner (2004) have termed 'familiarity-gated recollection,' whereby source retrieval attempts are confined to test items that are not initially judged to be novel.

In marked contrast to the insensitivity of behavioral measures to the probability manipulation, probability effects on brain activity were observed in several regions. Below, we discuss the possible functional significance of probability-sensitive and probability-insensitive fMRI retrieval-success effects and their relevance for recent proposals about the roles of left posterior parietal cortex and the medial temporal lobe in memory retrieval.

Regions showing retrieval success effects in the present study correspond to those reported many times previously (e.g., Wheeler & Buckner, 2004; Yonelinas et al., 2005; Johnson & Rugg, 2007; see Rugg & Henson (2002) for a review of early studies). Additionally, the regions where retrieval-related activity demonstrated an interaction between trial type and old/new ratio accord well with those reported by Herron, Henson, and Rugg (2004). According to the logic outlined in the Introduction, regions where retrieval success effects do not interact with old/new ratio are candidates for supporting retrieval operations per se, whereas regions where retrieval success effects interact with ratio are candidates for supporting processes operating downstream of retrieval. As in the study of Herron, Henson, and Rugg (2004), the present study dissociated regions within the left lateral parietal cortex according to whether activity in the regions was sensitive to old/new ratio. Importantly, by using a source memory paradigm, here we were further able to directly address the question whether the neural correlates of recollection are sensitive to old/new ratio. Three distinct patterns of retrieval-related parietal activity were observed. An area on the border of the left inferior lateral parietal and occipital cortex (BA 39/19) was sensitive to recollection (as operationalized by successful source retrieval) but not to old/new ratio. Two superior parietal regions, one anterior and one posterior to the middle IPS, showed probability-sensitive retrieval success effects. Finally, retrieval success effects in the middle IPS were modulated neither by recollection nor by old/new ratio. These findings suggest a functional division within the left lateral parietal cortex between

<sup>&</sup>lt;sup>3</sup>Even with the threshold for the interaction contrast reduced to p < 0.01, no significant clusters were evident within posterior parietal cortex.

regions supporting different retrieval operations (inferior lateral parietal cortex and middle IPS), and regions supporting processes downstream from, or contingent upon, successful retrieval (anterior IPS and posterior superior parietal cortex).

The findings for left inferior parietal cortex are in accord with those of prior studies in indicating a selective role for this region in recollection (e.g., Cansino et al., 2002; Wheeler & Buckner, 2004; Yonelinas et al., 2005; Woodruff et al., 2005; Vilberg & Rugg, 2007; 2008b; Johnson & Rugg, 2007), and with recent studies demonstrating strong resting functional connectivity between this region and the hippocampal formation (Vincent et al., 2006; 2008). Given the operational definition of recollection employed here (source correct > source incorrect/unsure), it is possible that the left inferior parietal activity associated with successful source recollection reflects sensitivity to the amount of information recollected, rather than to recollective processing more generally. This possibility arises because, on trials where source memory was unsuccessful, the test item might nonetheless have elicited recollection of details of the study episode that were non-diagnostic of source (so-called 'non-criterial' recollection). Support for this possibility comes from the finding that the present 'recollection-sensitive' left inferior parietal cluster overlaps with the region identified by Vilberg and Rugg (2007; 2008b) as sensitive to amount of information recollected (see Results). On the other hand, the finding that left inferior parietal activity elicited by items attracting incorrect or unsure source judgments (SI) and by correct rejections was equivalent (see Figure 5), lends support to the alternative possibility that this region was responding in the present study primarily to the occurrence of recollection, and not just to amount of information recollected. Regardless of which account is the more accurate, since the neural correlates of attentional reorienting are held to be probability-sensitive (Corbetta, Patul, & Shulman, 2008), the insensitivity of left inferior parietal recollection effects to old/new ratio is difficult to reconcile with the proposal that retrieval-related activity in this region is a reflection of this process (Ciaramelli, Grady, & Moscovitch, 2008; Cabeza et al., 2008; Cabeza, 2008). Rather, the findings are more consistent with the proposal (Vilberg & Rugg, 2007; 2008a; 2008b) that the region supports the representation or maintenance of the contents of recollection.

The present findings also shed further light on the possible roles in recognition memory of left superior parietal cortex in the vicinity of the IPS. Based in part on prior reports that this region is sensitive to the relative probability of 'target' stimuli in oddball tasks (Fichtenholtz et al., 2004; Kiehl & Liddle, 2003; Brazdil et al., 2007), we proposed (Vilberg & Rugg, 2008a) that retrieval success effects in the left middle IPS reflect the role of this region in detecting or responding to salient or behaviorally relevant stimulus events. By this argument, the retrieval success effects that are evident in this region reflect the fact that, in most recognition memory tests, 'old' items constitute relatively infrequent 'target' events, somewhat analogous to the target stimuli of an oddball task. As noted in the Introduction, we interpreted Herron, Henson, and Rugg's (2004) finding that left superior parietal 'retrieval success effects' are modulated by old/new ratio in that light. The present findings indicate, however, that our interpretation of that prior result was mistaken. Although we were successful in replicating the finding of an interaction between old/new ratio and left superior parietal activity, the regions demonstrating this interaction do not include the middle IPS region where retrieval success effects are typically reported (Wagner et al., 2005; Vilberg and Rugg, 2008a). As is evident from Figure 6, probability-sensitive left parietal regions were localized anterior and posterior to this middle IPS region. According to the logic outlined in the Introduction, therefore, it is these anterior and posterior regions, rather than the middle IPS, that are candidates for supporting the postretrieval, target-sensitive processes that we have previously proposed to be engaged during recognition memory tests.

What might be the functional significance of the retrieval-related activity identified in these different left superior parietal regions? The seeming insensitivity of the left middle IPS to old/

new ratio arguably poses difficulties for any proposal linking retrieval-related activity in this region to attentional processing (Ciaramelli, Grady, & Moscovitch, 2008; Cabeza, 2008), and suggests that the activity may be more directly related to retrieval than hitherto imagined. One possibility, originally put forward by Wagner et al. (2005), is that the region supports something akin to an 'accumulator', tracking the amount of evidence favoring an 'old' decision (Wixted, 2007). Such a function is arguably compatible with findings suggesting that this region of the IPS supports the abstract coding of magnitude (Piazza et al., 2007). It has also been proposed, however, that the middle IPS plays a direct role in retrieval. Takahashi, Ohki, & Kim (2008) reported yes/no recognition performance and functional connectivity between left middle IPS and left lateral temporal cortex were positively correlated, prompting the authors to propose that the role of the IPS in recognition is to retrieve representations of studied items that are 'stored' in other cortical regions.

The probability-sensitive anterior IPS region identified in the present study is in the vicinity of regions supporting representation and dynamic control of action (Tunik et al., 2007). Intriguingly, action-related activity in this region demonstrates 'repetition-suppression' (Hamilton & Grafton, 2006) for repeated versus novel actions. We conjecture that the present probability-sensitive retrieval effects identified in this region may, at least partially, reflect its contribution to the maintenance and execution of the different finger responses associated with old and new items. By this argument, anterior IPS activity is modulated both by the salience (or targetness) of the eliciting events, and the relative frequency with which a response is required to each event.

Whereas prior findings arguably offer some clues to the possible roles of the anterior and middle IPS in recognition memory, they shed little light on our findings for left posterior superior parietal cortex. In light of the multiplicity of functions that have been ascribed to IPS and immediately surrounding cortex, and the evidence for considerable functionally heterogeneity within this region (not only along its rostro-caudal axis, but also between the medial and lateral banks; Grefkes & Fink, 2005), we believe that additional research will be required before it is possible to fully specify the roles of this region in recognition memory and related tasks.

As in Herron, Henson, and Rugg (2004), the present study identified probability-insensitive New > Old effects in the MTL. In contrast to the prior finding, however, which was limited to a four-voxel cluster in right perirhinal cortex, here the effects were markedly more extensive. The present finding is also consistent with several other prior reports (Rugg, Henson, & Robb, 2003; Rombouts et al., 2001; Henson et al., 2003; Yassa & Stark, 2008; Johnson, Muftuler, & Rugg, 2008). As in some of these prior studies (e.g., Rugg, Henson, & Robb, 2003), the present effects were not confined to the extra-hippocampal anterior regions (in the vicinity of perirhinal cortex) where New > Old effects are often held to signal item familiarity (e.g. Aggleton & Brown, 2006; Henson et al., 2003). One possible explanation for the extension of the present MTL effects into hippocampus and entorhinal cortex is that this reflects the role of these regions in episodic encoding of novel information (Stark & Okado, 2003). We conjecture that in the present study adoption of the strategy of familiarity-gated recollection (see above) caused new items to be accorded high task relevance, potentiating their hippocampally-mediated encoding (Dudukovic & Wagner, 2007). Interestingly, these putative MTL novelty-sensitive encoding operations were unaffected by the manipulation of old/new ratio (see Figure 2).

In addition to the aforementioned New > Old effects, a more restricted region of the MTL (again including hippocampus), demonstrated relatively greater activity for source correct than for source incorrect test items (see Figures 2 and 5). This finding is consistent with several prior reports that the hippocampus and surrounding cortex are recollection-sensitive, as indexed by differences in the activity elicited by test items attracting correct versus incorrect source judgments (Cansino et al., 2002; Dobbins et al., 2003; Peters et al., 2007; Ross &

Slotnick, 2008), or 'Remember' versus 'Know' judgments (Woodruff et al., 2005; Fenker et al., 2005; Yonelinas et al., 2005; Johnson & Rugg, 2007; Vilberg & Rugg, 2007). Together with prior findings (e.g., Woodruff et al., 2005; Yonelinas et al., 2005), the present results highlight the fact that new item activity is not an appropriate 'baseline' against which to detect recollection-related activity in the MTL. As is clear from Figures 2 and 5, the same MTL regions (as far as can be ascertained at the spatial resolution of conventional fMRI) that respond differentially on the basis source accuracy are capable of responding even more strongly to item novelty. Finally, as was the case for MTL New > Old effects, MTL recollection-related activity was also insensitive to old/new ratio, as would be expected given the widely held view that this activity reflects processes that directly contribute to episodic retrieval. To our knowledge, this is the first demonstration that recollection-related hippocampal activity is insensitive to the probability of successful recollection.

In conclusion, we were able to identify three classes of functionally distinct, retrieval-related regions: one (that included left inferior parietal cortex and hippocampus) that showed selectivity for recollection and insensitivity to old/new ratio, another (including the middle intraparietal sulcus) that demonstrated generic retrieval success effects which also did not interact with old/new ratio, and a final class of regions (falling anterior and posterior to the middle IPS) where retrieval success effects interacted with old/new ratio. The results add further weight to the evidence that both left inferior lateral parietal cortex and the hippocampal formation support recollection, as operationalized by successful versus unsuccessful source retrieval. In addition, the findings indicate the need for further research to elucidate the functional significance of retrieval-success effects localized to superior parietal cortex in the vicinity of the middle IPS.

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#### Figure 1.

Regions where activity elicited by old items exceeded that for new items independently of old/ new ratio. The effects are displayed (left) on a rendered brain and (right) on a representative subject's section at x = -10.





#### Figure 2.

Top: Regions where activity elicited by new items exceeded that for old items independently of old/new ratio. Bottom: Mean peak parameter estimates (and standard errors) of regions A: left MTL (-27, -18, -24), B: right MTL (27, -15, -27), and C: medial orbitofrontal cortex (0, 57, -6) are plotted for each of the low and high old/new ratio blocks.



#### Figure 3.

Regions where activity demonstrated an interaction between trial type (Hit vs. CR) and old/ new ratio: (A) left dorsolateral prefrontal cortex (-54, 12, 39), (B) left anterior superior parietal cortex (-48, -27, 54), and (C) posterior superior parietal cortex (6, -75, 51).



# Figure 4.

Top: Clusters in the left superior parietal cortex where activity demonstrated an interaction between trial type (Hit vs. CR) and old/new ratio (left and right), and where retrieval success effects did not interact with ratio (middle) are displayed on sections of a representative subject. Cross-hairs identify the voxels for which parameter estimates were extracted. Bottom: For each cluster and old/new ratio, mean peak parameter estimates (and standard errors) are plotted for Hits and Correct Rejections (left) as well as SC and SI hits (right). Note that for the posterior superior parietal cluster, the parameter estimates are given for the subpeak located in the left superior parietal lobule.









# Figure 5.

Regions sensitive to recollection independent of old/new ratio (thresholded for display purposes at p < 0.005). Mean peak parameter estimates (and standard errors) of regions A: left inferior lateral parietal/occipital cortex (-36, -84, 27) and B: right anterior MTL (24, 0, -24) for each of the low and high old/new ratio blocks are displayed.



## Figure 6.

Retrieval success effects which were independent of old/new ratio (Red) and retrieval success effects which interacted with ratio (Green) are displayed on (left lateral and dorsal views of) rendered brains and a section at z = 52 of a representative subject.

#### Table 1

Mean proportions of source correct, source incorrect, and source unsure judgments for correctly recognized study items for each of the old/new ratio blocks

Block	Correct	Incorrect	Unsure
Low	0.62 (0.04)	0.22 (0.03)	0.16 (0.04)
High	0.64 (0.04)	0.19 (0.04)	0.17 (0.04)

Note. Standard error in parentheses.

# Test RT (ms) by old/new ratio

Old/New Ratio	SC	SI	CR	Miss
Low	1645 (233)	1808 (328)	1188 (183)	1485 (494)
High	1598 (254)	1753 (306)	1199 (185)	1380 (246)

Table 2

Note. Standard error in parentheses.

# Table 3 Regions showing retrieval success effects that were insensitive old/new ratio at test

Region	BA	НМ	Location	Peak Z (# vox)
Hit > CR				
Medial frontal gyrus	6/32	L/R	-6, 27, 51	5.66 (194)
	32	L	-9, 9, 51	3.20 (5)
Middle frontal gyrus	9	R	48, 27, 30	4.53 (29)
	6	R	36, 15, 51	4.10 (9)
	6	R	27, -3, 51	3.86 (18)
	6/8/9	L	-33, 6, 60	4.43 (166)
Inferior frontal gyrus	45	R	39, 24, -6	4.76 (67)
	44/46	L	-54, 15, 9	5.53 (488)
Anterior cingulated		R	12, 30, 21	3.72(10)
Putamen		L	-15, 9, -6	3.82 (6)
Midbrain		L/R	9, -15, -9	5.30 (387)
		L	-6, -30, -15	3.95 (13)
Thalamus		L	-9, -9, 3	4.72 (110)
Precentral gyrus	6	L	-42, -3, 30	4.12 (7)
Cingulate		L	-6, -30, 27	4.37 (15)
Inferior temporal gyrus	37	L	-60, -51, -15	5.03 (85)
Cerebellum		R	30, -39, -48	3.55 (6)
		R	30, -66, -36	4.36 (75)
		L	-39, -66, -39	3.23 (5)
Inferior parietal cortex	40	R	39, -48, 42	3.66 (19)
Sup./inf. parietal cortex	7/40/39/19	L	-33, -66, 48	5.62 (520)
Precuneus/post. cingulated	7/31	R	18, -57, 18	3.79 (14)
CR > Hit				
Medial frontal gyrus	10	L/R	0, 57, -6	4.34 (639)
Temporopolar cortex	38	L	-48, 9, -42	3.87 (13)
Nucleus accumbens		L/R	-3, 12, -12	3.90 (44)
Temporopolar cortex	38	R	39, 12, -48	3.50 (13)
Middle temporal gyrus	21	L	-57, -9, -21	4.51 (215)
Precentral gyrus	4/6	R	51, -9, 15	3.59 (5)
	4/6	R	15, -24, 63	4.51 (362)
Ant. medial temporal cortex		L	-21, -6, -27	3.87 (9)
Iinferior temporal gyrus	21	R	60, -6, -27	3.38 (20)
Hippocampus		L	-27, -18, -24	4.32 (37)
		R	27, -15, -27	4.16 (100)
Internal capsule		L	-18, -21, 30	3.93 (26)
		L	-21, -33, 30	3.34 (5)
Cingulate		L	-18, -30, 45	4.02 (5)
Insula		L	-42, -42, 21	4.86 (215)
Mid./sup. temporal gyrus	21/22/37	R	51, -66, 12	4.76 (443)

Region	BA	НМ	Location	Peak Z (# vox)
Middle occipital gyrus	18	L	-36, -72, 0	4.08 (99)

Z-values refer to peak activated cluster. Brodmann area (BA), hemisphere (HM), left (L), right (R).

# Table 4

# Regions showing an interaction between trial type (Hit vs. CR) and old/new ratio

Region	BA	HM	Location	Peak Z (# vox)
Dorsolateral prefrontal cortex	10/46	L	-27, 48, 6	4.03 (64)
	46	L	-42, 24, 24	3.22 (7)
Anterior cingulated	32	L	-18, 36, 24	3.73 (5)
Inferior frontal gyrus	9	L	-54, 12, 39	3.72 (42)
	9/44	L	-39, 9, 24	3.67 (21)
Superior frontal gyrus	6/8	L	-24, 3, 60	3.26 (15)
	6	L	-30, -6, 66	3.19 (17)
Anterior parietal/postcentral gyrus	40/2	L	-48, -27, 54	3.82 (148)
Inferior parietal cortex	40	R	45, -36, 36	2.96 (6)
Fusiform gyrus	37	R	54, -51, -24	3.49 (11)
Cerebellum		R	33, -57, -27	3.74 (7)
		R	12, -84, -33	3.63 (7)
Superior posterior parietal	7	L/R	6, -75, 51	4.44 (187)
	7	L/R	-6, -72, 3	3.18 (10)
Occipital	17	R	36, -87, -9	3.76 (73)

Z-values refer to peak activated cluster. Brodmann area (BA), hemisphere (HM), left (L), right (R).

# Table 5

# Regions sensitive to recollection and insensitive old/new ratio at test

Region	BA	НМ	Location	Peak Z (# vox)
Anterior medial temporal cortex	39/19	R	24, 0, -24	3.63 (5)
Inferior parietal/occipital cortex		L	-36, -84, 27	3.34 (9)

Z-values refer to peak activated cluster. Brodmann area (BA), hemisphere (HM), left (L), right (R).