

Functional Heterogeneity in Posterior Parietal Cortex Across Attention and Episodic Memory Retrieval

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While attention is critical for event memory, debate has arisen regarding the extent to which posterior parietal cortex (PPC) activation during episodic retrieval reflects engagement of PPC-mediated mechanisms of attention. Here, we directly examined the relationship between attention and memory, within and across subjects, using functional magnetic resonance imaging attention-mapping and episodic retrieval paradigms. During retrieval, 4 functionally dissociable PPC regions were identified. Specifically, 2 PPC regions positively tracked retrieval outcomes: lateral intraparietal sulcus (latIPS) indexed graded item memory strength, whereas angular gyrus (AnG) tracked recollection. By contrast, 2 other PPC regions demonstrated nonmonotonic relationships with retrieval: superior parietal lobule (SPL) tracked retrieval reaction time, consistent with a graded engagement of top-down attention, whereas temporoparietal junction displayed a complex pattern of below-baseline retrieval activity, perhaps reflecting disengagement of bottom-up attention. Analyses of retrieval effects in PPC topographic spatial attention maps (IPS0-IPS5; SPL1) revealed that IPS5 and SPL1 exhibited a nonmonotonic relationship with retrieval outcomes resembling that in the SPL region, further suggesting that SPL activation during retrieval reflects top-down attention. While demands on PPC attention mechanisms vary during retrieval attempts, the present functional parcellation of PPC indicates that 2 additional mechanisms (mediated by latIPS and AnG) positively track retrieval outcomes.

Keywords: dual attention theory, fMRI, familiarity, recollection, topographic mapping

Introduction

An ongoing debate that spans multiple subfields of cognitive neuroscience surrounds the precise computations performed by lateral posterior parietal cortex (PPC). Because this region is consistently implicated in a vast array of tasks—from attention and numerical cognition to decision-making and action intention—it has proven difficult to identify the shared and distinct computational processes supported by PPC that account for its participation in these widely varied domains. Recently, memory researchers have also turned their attention to the role of PPC in cognition because human neuroimaging experiments have consistently revealed PPC activity during episodic retrieval (Wheeler and Buckner 2004; Wagner et al. 2005; Cabeza et al. 2008; Ciaramelli et al. 2008; Vilberg and Rugg 2008b; Olson and Berryhill 2009). Moreover, studies of human patients with lesions to PPC have revealed subtle, but significant, memory impairments (Berryhill et al. 2007; Davidson et al. 2008; Berryhill et al. 2010; Ciaramelli et al. 2010; Drowos et al. 2010; Simons et al. 2010, cf. Ally et al. 2008;

Haramati et al. 2008; Simons et al. 2008). Several hypotheses have been advanced to account for the role of PPC in episodic retrieval, including interpretations based on attention, decision-making, episodic buffering, and relational binding (Wagner et al. 2005; Cabeza et al. 2008; Vilberg and Rugg 2008b; Shimamura 2011). Empirical tests of the predictions of these disparate accounts remain nascent (Ciaramelli et al. 2010; Sestieri et al. 2010), and thus, the underlying computations performed by PPC during retrieval remain unresolved.

Interpretation of PPC function during remembering is complicated by the fact that multiple mnemonic processes contribute to episodic retrieval and seem to differentially elicit activity in PPC. Specifically, although early electroencephalography and functional magnetic resonance imaging (fMRI) studies of recognition memory emphasized elevated signals in left PPC during the correct identification of items previously encountered as “old” (i.e., hits) versus the correct identification of novel items as “new” (i.e., correct rejections), it is now largely accepted that PPC “old/new effects” are comprised of at least 2 anatomically separable components (for reviews, see Wagner et al. 2005; Rugg and Curran 2007). The dorsal component consists of regions in and along the intraparietal sulcus (IPS) and superior parietal lobule (SPL) in which activity is thought to track differences in item memory strength or “familiarity”—a sense of having encountered an item before, unaccompanied by the retrieval of additional contextual details (It should be noted that the use of the term “dorsal” to describe IPS and nearby regions here and elsewhere is meant to disambiguate the region from the more ventral regions of PPC which have been argued to play a role in recollection and bottom-up attention. That is, describing IPS as dorsal is intended here as a relative reference, rather than as a formal anatomical label of superior versus inferior parietal lobules.). The ventral component is commonly centered on the angular gyrus (AnG) and/or supramarginal gyrus (SMG) and is thought to relate to “recollection”—the subjective sense and/or objective evidence of having retrieved details from a prior event (Yonelinas 2002; Wheeler and Buckner 2004; Wagner et al. 2005; Cabeza 2008; Cabeza et al. 2012; cf. O’Connor et al. 2010). For example, Yonelinas et al. (2005) reported enhanced blood oxygen level-dependent (BOLD) activity in SMG when participants reported the subjective sense of having recollected contextual details from a study episode, as well as activity in a more dorsal region that displayed a graded increase in magnitude as a function of item memory strength (confidence that the test probe was old).

Given these 2 distinct left PPC retrieval effects, attempts to specify the PPC operations that support retrieval have relied

on coarse-grained, 2-process models. A particularly influential account (Cabeza et al. 2008; Ciaramelli et al. 2008) posits that the dorsal/ventral distinction observed in the episodic memory literature reflects the recruitment of the dorsal, “top-down” and ventral, “bottom-up” attention networks articulated by Corbetta and coworkers (Corbetta and Shulman 2002; Corbetta et al. 2008). From this perspective, greater activity during hits versus correct rejections in dorsal PPC is posited to reflect the role of top-down attention in facilitating memory reinstatement and memory-based decisions, whereas old/new effects in ventral PPC are posited to reflect the reorienting of attention to behaviorally relevant event details retrieved from memory.

To date, there have been several efforts to test this “attention to memory” account. Ciaramelli et al. (2010) described neuroimaging and neuropsychological data from a cued recognition paradigm suggesting that dorsal and ventral PPC are involved in top-down and bottom-up attention to memory, respectively. Cabeza et al. (2011) reported dorsal PPC activity associated with attentional orienting during both a memory task and an attention task, as well as overlap of activity in ventral PPC during the immediate pre-response period across the 2 tasks. Although these studies are suggestive of how attention and retrieval processes might interact, it is difficult to draw strong conclusions about this interaction because of 3 factors: First, the former study did not collect any measures of perceptual attention, thus limiting the ability to assess similarities and/or differences in localization. Second, the latter study did not report neuroimaging effects associated with memory outcome (i.e., old/new effects), again limiting the assessment of attention/memory overlap. Finally, while this latter study focused on overlap, it also showed anatomical divergence of the attention and memory effects, making the correspondence across the domains less clear.

The attentional account of PPC retrieval effects, while conceptually attractive at a number of levels, has been challenged by recent meta-analytic (Hutchinson et al. 2009) and within-study (Sestieri et al. 2010, 2011) evidence that suggests that the PPC subregions associated with top-down and bottom-up attention are anatomically separable from those associated with episodic retrieval (see also Shannon and Buckner (2004) for evidence of further visuospatial attention/retrieval dissociations). For example, drawing on the published attention and memory literatures, Hutchinson et al. (2009) systematically assessed the overlap in PPC between effects of top-down and bottom-up attention and those of item memory strength and recollection. While the spatial resolution of the implemented meta-analytic approach was inherently limited, Hutchinson’s findings suggest that memory strength effects in dorsal PPC may be located lateral to top-down attention effects and that recollection effects in ventral PPC may be located posterior to bottom-up attention effects. In a direct empirical comparison, Sestieri et al. (2010) assessed PPC involvement in a perceptual search task and a memory search task. Although the memory search task was not designed to reveal regions differentially involved in item memory versus recollection, the results of this study aligned with the aforementioned meta-analysis, suggesting minimal overlap between memory-related and attention-related effects in PPC. Taken together, these findings suggest that a coarse, dorsal/ventral axis of organization that directly maps memory effects

(i.e., item memory strength/recollection) to attention effects (i.e., top-down/bottom-up) is insufficient to explain extant PPC retrieval data.

Interpretation of PPC functional specialization during episodic retrieval also requires consideration of the growing literature demonstrating that PPC contains a mosaic of subregions, each with unique connectivity, functional properties, and receptor composition (Zilles and Palomero-Gallagher 2001; Greffkes and Fink 2005; Silver and Kastner 2009; Uddin et al. 2010; Uncapher et al. 2010; Nelson et al. 2010; Mars et al. 2011; Sestieri et al. 2011; Yeo et al. 2011; Caspers et al. 2012). In light of the debate regarding PPC contributions to attention and memory, a particularly relevant aspect of this recent research has been the discovery and characterization of topographically organized maps of attended visual space in IPS and SPL (for review, see Silver and Kastner 2009). These maps have provided researchers with a more detailed understanding of information representation in dorsal parietal cortex. Moreover, because the locations and boundaries of these maps can be objectively identified in each subject based on their visual field representations, these areas also serve as reliable landmarks in guiding research on functional specialization within PPC. Although topographic areas in IPS and SPL have been associated broadly with the deployment of top-down spatial attention (Silver and Kastner 2009), there is also meaningful heterogeneity among them (Konen and Kastner 2008a, 2008b; Sheremata et al. 2010), and it is unknown how these regions are engaged, either uniformly or differentially, during complex cognitive acts such as episodic retrieval. Indeed, while initial efforts to parcellate PPC with respect to episodic retrieval have indicated anatomical separation between parietal regions involved in top-down attention and memory (Sestieri et al. 2010, 2011; see also Nelson et al. 2010), no study to date has examined the anatomical and functional correspondences between PPC regions involved in retrieval and topographic parietal visual field maps. Thus, the relationships between parietal regions thought to index item memory strength (familiarity) and recollection and the multiple topographic maps of attended space remain unclear.

The current study aimed to delineate, within-experiment and within-subject, the functional subunits within PPC and their roles in memory and attention using a 2-pronged approach. First, we implemented an episodic retrieval task that allowed for a fine-grained analysis of episodic remembering, providing a rich set of memory behaviors that were used to functionally parcellate PPC activity. This approach revealed a quadruple functional dissociation in left lateral PPC during retrieval. Second, to directly examine the relationship between these 4 effects and topographic maps of attention, we systematically mapped top-down, spatial attention-related activity in PPC in a subset of the participants from the memory experiment and related the obtained attention maps to the retrieval effects. Specifically, we identified 7 discrete representations of attended visual space (IPS0-IPS5 and SPL1; Silver and Kastner 2009), affording a fine-grained within-subject investigation of the relationships between PPC top-down attention and episodic retrieval effects. Given substantial individual variability in the size and location of these topographic PPC areas (Silver and Kastner 2009), we conducted 1) memory/attention overlap analysis on an individual-subject basis and 2) analyses

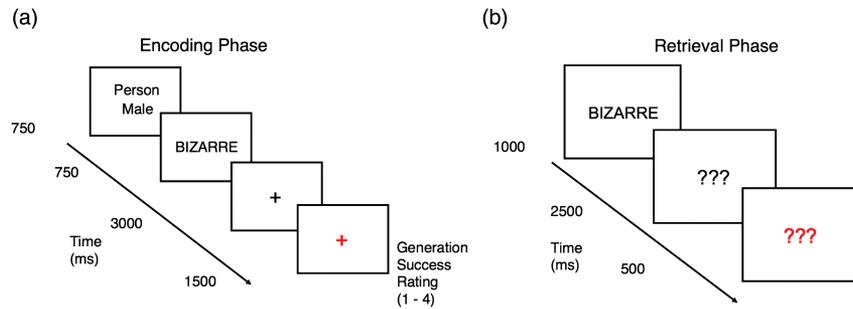


Figure 1. Experimental trial structure. (a) Schematic of a single trial during the prescanning encoding phase. Participants were cued to generate an instance of a male or female celebrity (person generation task) or an indoor or outdoor scene (scene generation task). At the end of each trial, a red fixation cross signaled participants to report their success in generating a person or scene described by the adjective. (b) Schematic of a trial during the scanned retrieval phase. Question marks changed from black to red 500 ms before the end of the trial. Participants were presented with either a previously studied or a novel word and then made 1 of 8 possible memory responses (Table 1).

of task-evoked responses from the memory task within each topographic area.

We began by characterizing the rich array of operations engaged during retrieval using a graded memory task ($N=19$). This task assessed recognition accompanied by different levels of contextual recollection, as well as acontextual item recognition (Fig. 1 and Table 1). Participants completed an encoding task outside the scanner and then a retrieval task while being scanned. During each trial of the encoding phase, subjects were presented with an adjective and asked to use that word to generate a mental image of 1) an indoor scene or 2) an outdoor scene, or to generate the name of 3) a famous male or 4) a famous female. During each trial of the scanned retrieval phase, subjects were presented with either a previously seen or a novel adjective. Subjects made 1 of 8 responses, indicating whether they: remembered specific contextual details of the study episode (i.e., whether they had used the adjective to generate 1) an indoor or 2) outdoor scene, or 3) a famous male or 4) female); remembered task-level contextual details (i.e., whether they had used the adjective to generate 5) a scene or 6) a person, with no further level of recollection specificity); experienced acontextual item recognition (i.e., recognized the word as having been studied, but without 7) recollection of contextual details); or perceived the adjective as 8) novel.

Following the memory experiment, 5 of the participants were scanned using the spatial attention mapping procedure. This procedure defined, within each hemisphere of each subject, maps along the IPS0-IPS5 and in the SPL1 associated with the allocation of top-down spatial attention (Tootell et al. 1998; Sereno et al. 2001; Silver et al. 2005; Swisher et al. 2007; Konen and Kastner 2008a; Silver and Kastner 2009). The attention maps were then compared with the retrieval effects observed in these participants (see Methods and Results sections), allowing us to directly evaluate which, if any, regions containing topographic attention maps are recruited during episodic retrieval. We found that human lateral PPC is comprised of multiple functional substructures, some of which are associated with distinct aspects of episodic memory retrieval and others with the allocation of visuospatial attention. Critically, those associated with recollection and item memory appear separable from those associated with attention. In addition, some of the regions containing topographic attention maps expressed a pattern of activity consistent with the engagement of top-down attention during episodic retrieval.

Table 1

Test phase response option and experimental condition (retrieval outcome)

Response	Item History	Retrieval Outcome
'New'	Novel	Correct Reject
'New'	Scene or Person Task	Miss
'Old'	Scene or Person Task	Item Only
'Scene'	Scene:Indoor or Outdoor	Task Source
'Person'	Person:Male or Female	Task Source
'Indoor'	Scene:Indoor	Specific Source
'Outdoor'	Scene:Outdoor	Specific Source
'Male'	Person:Male	Specific Source
'Female'	Person:Female	Specific Source

Subjects' responses were conditioned on the retrieval outcome. The left column lists the 8 possible responses, and the right column lists the descriptive label for each mnemonic category.

Methods

Participants

Twenty-six healthy adults participated in the memory portion of the study. Participants were right-handed, native English speakers, with no history of neurological disease or contraindications for MR imaging. Data from 4 participants were excluded due to imaging artifacts; data were also excluded from one participant due to excessive movement and from 2 additional participants due to poor recognition memory ($d' < 0.3$). Accordingly, memory data from 19 participants were analyzed (11 female, ages 18–28 years). Of these participants, 5 returned for a follow-up attention mapping experiment (1 female, ages 21–27 years). Participants were compensated \$10/h for behavioral testing and \$20/h for scanning sessions. The memory experiment lasted approximately 3.5 h, and the attention mapping experiment lasted approximately 3 h (1 h for behavioral practice and 2 h for fMRI scanning). All participants gave informed written consent in accordance with procedures approved by the Institutional Review Board at Stanford University.

Procedure

Graded Memory Experiment

The graded memory experiment consisted of 2 phases: an encoding phase administered outside of the scanner and a retrieval phase conducted during fMRI scanning. Each phase was preceded by a brief practice round containing a set of trials with identical structures to the actual task. The retrieval phase was additionally preceded by a response training session, wherein participants practiced making the 8 responses that would be used during retrieval. The interval between the end of encoding and the beginning of retrieval was approximately 20–30 min.

Stimuli consisted of 620 visually presented adjectives, taken from a corpus used in 2 prior fMRI studies (Davachi et al. 2003; Kahn et al. 2004). The adjectives ranged in length from 3 to 10 letters (mean = 6.93). Twenty adjectives were used during practice. Of the 600 remaining items, 400 were presented during the encoding phase and served as old items during the retrieval phase, and 200 served as novel items (foils) during retrieval. During encoding, there were 100 items in each of 4 encoding conditions (person: male, person: female, scene: indoor, and scene: outdoor). Trial order was pseudorandomized so as to not contain more than 3 consecutive trials of a given condition. During retrieval, the order of retrieval probe types (i.e., the 4 types of old stimuli as well as novel foils) was determined using the OptSeq algorithm (Dale 1999). The algorithm also determined the duration and frequency of null (fixation) events, which accounted for approximately one-third of trials. The retrieval phase was composed of 10 blocks of 60 trials each. Each block lasted 6 min and 24 s, and the entire experiment (including encoding) lasted approximately 3 h. Across participants, stimuli were counterbalanced across the 4 encoding conditions and could serve as either studied or novel items at retrieval.

In the encoding phase, each trial began with presentation of a task cue (750 ms), followed by an adjective (750 ms), a delay (3000 ms), and a response period (1500 ms) (Fig. 1*a*). One of 4 task cues prompted participants to covertly generate an instance of 1 of 4 types of referents best described by the subsequently presented adjective: the task cues "Person: Male" and "Person: Female" prompted covert generation of the name of a male or female celebrity, respectively, whereas the cues "Scene: Indoor" and "Scene: Outdoor" prompted generation of a mental image of an indoor or outdoor scene, respectively. The subsequent stimulus period displayed an adjective in capitalized black letters on a white background. Participants were given 3750 ms to generate a specific scene or person (stimulus and delay periods). During the delay period, a black fixation cross replaced the adjective and then turned red to instruct participants to make a response reflecting their generation success rating for that trial. Participants made 1 of 4 button presses describing their generation success: successful with ease, successful with effort, partially successful, or completely unsuccessful. Only items that received a rating of partially successful or better were analyzed in the subsequent test phase.

Following the encoding phase, participants were informed that their memory for the studied words would be tested during scanning and were then given instructions for the response training session and test phase. Participants performed the response training session while anatomical MR images were acquired. During the training session, verbal labels of the responses required during the test phase (see below) were visually presented one at a time at fixation, cycling through all 8 possible responses in random order. Labels were presented in black letters on a white background for 1000 ms. Participants were instructed to make a button press on each trial that mapped to the appropriate response and were given visual feedback after every trial. When they made a correct response, a diagram of the 2 4-button response boxes was presented, with the appropriate response highlighted in green. When an incorrect response was made, the appropriate response was highlighted in red. The training session continued until the participant responded correctly to the entire response set at least twice (minimum of 16 consecutive correct trials).

After completion of the training session, the test phase began. For each test trial, an old or new word was centrally presented in black text on a white background for 1000 ms, followed by a set of black question marks for 2500 ms (Fig. 1*b*). The end of the trial was signaled by the black question marks turning red for 500 ms, and participants could respond at any point during the trial. Participants were instructed to make 1 of 8 responses that best characterized their memory for the item (Table 1). Specifically, if participants believed that they recalled specific information about what they had generated during the encoding phase, they were instructed to make the appropriate response: "Male," "Female," "Indoor," or "Outdoor." If participants believed that they recalled which task they had performed but failed to recall further specific information (e.g., they remembered that they had generated a person's name in response to the adjective but did not recall the gender of the person), they were to respond either "Person" or "Scene." If participants were unable to recall either specific or task source information but

recognized the word as having been presented during the encoding phase, they were to respond "Old." Finally, if the participant did not recognize the word as having been presented during encoding, they were to respond "New." When participants were unsure, they were instructed to make their best guess. Periods in between trials (null events) consisted of a black fixation cross on a white background.

Attention Mapping Experiment

The stimulus and task in the attention mapping procedure were modeled after those used previously (Bressler and Silver 2010). During fMRI, a black and white, contrast-reversing (7.5 Hz) checkerboard wedge stimulus was continuously presented on a gray background, systematically rotating about a central fixation point (Engel et al. 1994; Sereno et al. 1995; Engel et al. 1997). The check size within the stimulus was scaled according to the cortical magnification factor in human V1 (Slotnick et al. 2001; Bressler and Silver 2010), and the stimulus contrast was 100%. The wedge subtended 45° and extended from 0.5° (inner radius) to 16° (outer radius) of visual angle, except when the wedge was at the top and bottom of the field of view (the dimensions of the mirror used for stimulus viewing extended 13° from fixation along the vertical meridian). The wedge rotated in 22.5° increments in a clockwise direction over 16 wedge positions, each overlapping 50% with its neighboring positions. The wedge completed a full rotation once every 34.133 s (2.133 s in each position).

During an initial behavioral training session and in the main experiment, participants were instructed to maintain fixation on a central point flanked by the rotating checkerboard wedge and to press a button whenever they detected a target within the wedge. The target was a square region of zero contrast (luminance equal to mean luminance of the wedge), presented for 270 ms (one full cycle of contrast-reversal of the checkerboard wedge stimulus). There was a 50% probability of target presentation at each wedge position, and the target could appear anywhere within the wedge stimulus at unpredictable times. This spatial and temporal uncertainty regarding target presentation encouraged participants to continuously maintain spatial attention over the entire rotating wedge. The target sizes in 3 eccentricity bands (0.5–5.7, 5.7–10.8, and 10.8–16° of visual angle) were scaled to equate target detection performance for these bands, but the boundaries between the eccentricity bands were not visible to the participants. Portions of the wedge not visible to the participant did not contain a target (i.e., the outer 3° of the wedge when it appeared along the vertical meridian). When necessary, the sizes of the targets were adjusted during the experiment to maintain participant performance at approximately 80% of targets correctly detected. Eye movements were not recorded during the fMRI experiment; however, all participants practiced maintaining fixation during the behavioral practice session.

For both the memory and the attention mapping experiments, stimulus presentation and collection of behavioral responses were implemented in Matlab, using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997) running on an Apple MacBookPro laptop. During the encoding phase of the memory experiment (conducted outside of the scanner), stimuli were centrally presented on the laptop monitor, and responses (button presses) were made on the laptop keyboard. During the scanned memory retrieval phase and attention mapping, stimuli were projected onto a screen and viewed through a mirror on the head coil, and responses (button presses) were made using either one (attention mapping) or 2 (memory experiment) MR-compatible response boxes. The assignment of responses to each hand was counterbalanced across participants in the memory experiment. All responses in the attention mapping procedure were made with the right hand.

fMRI Data Acquisition

All anatomical and functional data were acquired using a 3.0T Signa MRI system (GE Medical Systems). For the memory experiment, the first anatomical series was collected using a T_2 -weighted flow-compensated spin-echo pulse sequence (TR = 4.5 s; TE = 85 ms; 22 contiguous 5-mm-thick slices parallel to the AC-PC plane) with a prescription identical to that of the functional images. The second anatomical series was a T_1 -weighted high-resolution acquisition of the

entire brain (TR = 8.368 ms; TE = 1.784 ms; flip angle = 15°; FOV = 22 cm; 256 × 256 voxels; 124 contiguous 1.5-mm-thick slices). For all participants except one, functional images were collected using a T_2^* -weighted 2D gradient echo spiral-in/out pulse sequence (TR = 2 s; TE = 30 ms; 1 interleave; flip angle = 75°; FOV = 22 cm; 64 × 64 voxels). For a single participant, data were acquired at a slightly higher resolution (29 contiguous 4-mm-thick slices, with a 21-cm FOV).

For the attention mapping experiment, the anatomical series was collected using a T_2 -weighted flow-compensated spin-echo pulse sequence (TR = 4.5 s; TE = 85 ms; 30 contiguous 3-mm-thick coronal slices covering the posterior half of the brain) with a prescription identical to that of the functional images. Functional images were collected using a T_2^* -weighted 2D gradient echo spiral-in/out pulse sequence (TR = 2.133 s; TE = 30 ms; 1 interleave; flip angle = 75°; FOV = 20 cm; 64 × 64 voxels).

fMRI Data Analysis

Graded Memory Experiment

Data were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London). The first 6 TRs were discarded, and functional volumes were corrected for slice acquisition timing differences and were then motion corrected. For each participant, the high-resolution structural volume was co-registered to an average of the functional volumes and then segmented into cortical gray matter, white matter, and cerebrospinal fluid. The gray matter volume was normalized to the MNI gray matter template, and the resulting normalization parameters were applied to the functional volumes. Functional volumes were resampled into 3-mm³ voxels and smoothed with an 8-mm full-width half-maximum isotropic Gaussian kernel.

Statistical analyses were performed using the general linear model (GLM). For all analyses, each trial was modeled as a single event (i.e., stick function) at stimulus onset (i.e., the appearance of the word), and convolved with a canonical hemodynamic response function (HRF). A total of 4 models were run: the first explored the memory effects of interest using an odd/even split-half analysis to permit unbiased statistical testing at the ROI level; the second assessed how activity varied with reaction time (RT); and the third and fourth investigated whether the effects of interest were influenced by encoding task. With the exception of the RT model, temporal and dispersion derivatives were included in the analyses (Friston et al. 1998). For all models, the scanning sessions were concatenated, and the condition regressors were entered into a GLM with session and movement parameters as covariates (see below for details). Each time series was high-pass filtered to remove low-frequency drift (1/128 Hz and below). First-level linear contrasts were calculated to produce estimates of effects for each participant; these estimates were then entered into a second-level analysis in which participant was treated as a random effect. One-sample *t*-tests against a contrast value of zero were performed for each voxel. There were 5 critical memory retrieval regressors of interest: "Correct Rejections," "Misses," "Item Only," "Task Source," and "Specific Source" trials. For Item Only, Task Source, and Specific Source, only correct trials were included in the regressor. Nuisance regressors were included for noncritical events (incorrect Specific and Task Source responses and false alarms) and for events of no interest (i.e., when the participant did not make a response and trials for which participants were unable to generate an associate at study).

In our primary analysis (the first model), a voxel-level analysis was conducted to functionally define regions of interest (ROIs) which were then used to statistically assess the effects of retrieval. This analysis approach was adopted because tests for significant interactions between brain region and retrieval outcome are required to determine whether functionally distinct retrieval effects are present in separable parietal subregions. Critically, to perform statistically independent analyses on the extracted ROI data (i.e., analyses that are unbiased by voxel selection), we used a split-half analysis approach. Specifically, odd and even trials for all conditions of interest were modeled separately (correlation analyses on the modeled predictor time series between the odd and even events within each condition of interest confirmed the absence of a relationship between the 2 halves

of the data: the across-subject mean *r* ranged across conditions from −0.05 [for Misses] to −0.09 [for Item Only] and the mean *r*² was below 0.01 for all conditions).

Whole-brain voxelwise analyses were then performed on the odd trials to define ROIs with a voxel-level uncorrected threshold of all $P < 0.001$ and a cluster extent threshold of 5 or more contiguous voxels. We did not perform a correction for multiple statistical comparisons because the outcomes of the voxel-level comparisons were directly replicated in the subsequent ROI analyses using independent data, thus providing a within-experiment replication of the effects. ROIs included all significant voxels within an 8-mm radius of the peak voxel. Using the even trials, we then computed the hemodynamic response for each condition from these functionally defined ROIs. Deconvolution of the hemodynamic response within ROIs was performed using a finite impulse response function implemented in MarsBar (<http://marsbar.sourceforge.net/>). For each condition and each participant, integrated percent signal change was computed from these extracted response functions, summing over the 4–10-s poststimulus onset period (i.e., TRs 3–5). The resulting data were submitted to analyses of variance (ANOVA) and post hoc paired *t*-tests.

A second model implemented a parametric modulation analysis to detect regions where activity varied according to trial-by-trial RT. Here, each retrieval condition (Specific Source, Task Source, Item Only, Misses, and Correct Rejections) was modeled separately, and orthogonal regressors modulated each of these condition regressors according to the RT associated with each item in the regressor. The RT regressors permitted the identification of voxels in which activity varied as a positive linear function of RT on each trial, for each condition. All other events were modeled as a separate regressor of no interest.

Finally, because the ratio of items originating from the person generation or scene generation tasks varied by retrieval condition (see Supplementary Results), we constructed 2 additional "control" models to assess whether the differences between retrieval conditions observed in the primary model were driven by encoding task effects rather than retrieval processes per se. The first control model randomly subsampled items, equating the number of items from the 2 encoding tasks (Scene or Person) contributing to each retrieval condition (i.e., Misses, Item Only, Task Source, and Specific Source; Correct Rejections did not have corresponding encoding events). The second control model coded trials according to both retrieval condition and encoding task and examined if the parietal regions observed in the primary model displayed a retrieval condition by encoding task interaction. Both control analyses indicated that the effects of retrieval observed in the primary model were not due to encoding task differences (see Supplementary Results for details).

Attention Mapping Experiment

The attention mapping data were analyzed using mrVista (<http://white.stanford.edu/software/>). The first 4 TRs of each functional run were discarded, and each of the resulting 128-TR time series was corrected for motion, high-pass filtered, and converted to percent signal change. Each participant completed between 10 and 14 runs (3 runs were excluded from analysis in one participant due to motion-correlated noise). The duration of the stimulus cycle was 34.133 s, resulting in a modulation of fMRI signals of 0.029 Hz in responsive voxels. The coherency between a sinusoid of this frequency and the average fMRI time series for each voxel was calculated for each fMRI run (Rosenberg et al. 1989; Engel et al. 1994). Computation of coherency generates 2 quantities. The first is the coherency magnitude (coherency), or the strength of coupling between the best-fit sinusoid and the fMRI time series, and takes values between 0 and 1. The second quantity is the response phase, or the temporal phase of the best-fit sinusoid relative to the stimulus cycle. The response phase is used to estimate the angular component (in polar coordinates) of the visual field location that is represented by a given voxel. It should be noted that coherency as employed here is not the same as coherency between 2 fMRI time series (e.g., Lauritzen et al. 2009).

The boundaries of visual field representations in posterior parietal areas IPS0-5 and SPL1 were defined using established phase-encoded retinotopic mapping methods (Engel et al. 1994; Tootell et al. 1998;

Silver et al. 2005; Swisher et al. 2007; Konen and Kastner 2008a; Bressler and Silver 2010; Szczepanski et al. 2010). Maps were defined with a coherence threshold of 0.15 for each subject, a value that is consistent with prior work (e.g., Brewer et al. 2005). The time series obtained for each voxel were averaged across all runs, and cortical area boundaries were defined based on this average time series. The response phase was calculated for each voxel and then spatially transformed into computationally inflated cortical meshes (Fig. 5). Surface-rendered phase maps were examined by 2 experienced raters (KSW and DWB) who defined the locations and boundaries of the parietal maps based on guidelines in the published literature (Silver et al. 2005; Swisher et al. 2007; Konen and Kastner 2008a; Szczepanski et al. 2010). Critically, the areal boundaries were defined blind with respect to the retrieval data obtained from the 5 participants in the attention mapping experiment. The visual field maps were of sufficient quality to allow identification of the boundaries of all 7 parietal areas in both hemispheres of all participants, with the exception of SPL1 in a single participant's right hemisphere.

To facilitate comparisons between the memory and the attention mapping experiments in each subject, data from the memory experiment were reanalyzed, using mrVista, for the participants who completed attention mapping. Specifically, we generated individual participant voxelwise maps of retrieval effects, permitting projection of participant-specific memory and attention effects on a common surface in the participant's native brain space (Fig. 5b). For the voxelwise memory analyses, functional data were corrected for motion and high-pass filtered to remove low-frequency noise (1/128 Hz and below). A GLM was constructed with identical conditions of interest as in the first model above (however, odd and even events were not separated for this analysis). Each event was convolved with a gamma-parameterized HRF (Boynton et al. 1996), and first-level linear contrasts were calculated to produce estimates of effects for each participant, thresholded at all $P < 0.001$ (uncorrected). For visualization purposes, the group-level ROIs defined in the primary model above were also reverse-normalized to participant-specific anatomical space and rendered on the mrVista-derived surface (Fig. 5c).

To statistically assess the effects of memory within the ROIs (e.g., IPS0-5, SPL1) given the limited sample size, bootstrapping procedures were implemented. For each ROI, we first used a 2-step approach to assess whether there was a significant difference across memory conditions. For the first step, we computed the hemodynamic response for each condition, using a similar approach as in the group-level memory ROI analyses (i.e., GLM with identical conditions of interest as in the first model above [odd and even events were not separated]; data extracted via MarsBar; integrated percent signal change as the dependent measure). For each subject, individual event onsets were then randomly shuffled across condition membership (for the critical memory conditions of Correct Rejections, Misses, Item Only, Task Source, and Specific Source). This was done 1000 times for each ROI and each subject in order to generate null distributions of evoked response amplitudes for each condition. For the second step, an F value was calculated for the main effect of memory condition from the repeated measures ANOVA, using a randomly selected set of values from each subject's bootstrapped null distribution. This was repeated 10 000 times for each ROI to generate a second-level null distribution of F values. The F value from the actual recorded data for each ROI was then assigned a P value corresponding to the proportion of all bootstrapped F values that were of greater magnitude.

When significant main effects of memory condition were obtained, we then assessed whether specific pairwise differences between conditions were significant within an ROI, using a similar 2-step approach as above. For a given pairwise contrast, individual event onsets were randomly shuffled between the 2 conditions of interest. This was done 1000 times for each ROI and each subject in order to generate null distributions of the difference in evoked response amplitude between the 2 conditions. For the second step, the across-subject mean of the differences between conditions was calculated from randomly selected values taken from each subject's bootstrapped null distribution. This was repeated 10 000 times for each ROI to generate a second-level null distribution of average difference values. The actual difference between conditions for each ROI was then assigned a

P value corresponding to proportion of all bootstrapped difference values that were of greater magnitude (i.e., the proportion of absolute values that were greater than the absolute observed value). Owing to the intensive computation required for these analyses, they were conducted only for 4 comparisons of primary interest: "Item Only vs. Correct Rejections," "Task Source vs. Specific Source," "Task Source vs. Item Only," and "Specific Source vs. Item Only."

Finally, a third bootstrapping technique was used to test for significant region by condition interactions between pairs of ROIs. For a given set of ROIs, the observed values for each condition were shuffled for each subject and ROI, and the F statistic from the repeated measure 2-way ANOVA was calculated. This was repeated 10 000 times to generate a null distribution of F values and the actual F value of the interaction was then assigned a P value corresponding to the proportion of all bootstrapped F values that were of greater magnitude.

Results

Behavioral Performance

Graded Memory Experiment

Encoding phase. Participants successfully generated referents for the vast majority of the studied words. Specifically, person or scene generation was rated as "successful with ease" on 39.6% of trials [standard deviation (SD): 13.5%], "successful with effort" on 28.4% (SD: 9.9%), "partially successful" on 18.8% (SD: 6.4%), and "completely unsuccessful" on 13.3% (SD: 7.9%). This distribution did not vary by encoding task (person vs. scene; all $F_{3,54} = 1.07$, all $P > 0.3$). Retrieval trials associated with words rated as "completely unsuccessful" during encoding were excluded from behavioral and fMRI analysis.

Retrieval phase. Items presented during the encoding phase were considered correctly recognized (hits) if they generated any of the 6 source memory responses or the Old response (Table 1). The mean hit rate was significantly higher than the false alarm rate (all $t_{18} = 12.09$, all $P < 0.001$; Fig. 2a), and d' (mean = 1.08; SD = 0.35) differed from zero ($t_{18} = 13.26$, all $P < 0.001$), demonstrating that participants were able to discriminate old from new words. Similarly, when considering only Old and New responses (i.e., excluding trials on which source memory was expressed; computing hit and false alarm rates corrected for the opportunity to make an Old response; [Yonelinas and Jacoby 1995; Davachi et al. 2003; Kahn et al. 2004]), the hit rate (0.58) was significantly greater than the false alarm rate (0.31; $t_{18} = 10.21$, all $P < 0.001$). Recognition accuracy (d') did not change as a function of retrieval block (all $F_{9,162} = 1.192$, all $P > 0.3$), and d' did not differ across the first and last retrieval blocks (all $P > 0.1$), indicating that subjects maintained performance throughout the retrieval task.

The proportions of correctly recognized study items that corresponded to Item Only, Task Source, and Specific Source responses differed (all $F_{2,36} = 3.43$, all $P < 0.05$; Fig. 2a), and the distributions varied depending on whether participants had generated a scene or a person at study (see Supplementary Results for details). Source memory accuracy was calculated by determining the probability of a correct source response given that a source response was made to an old item. Task Source accuracy ($P_{\text{correct Task Source response} | \text{Task source response made to old item}}$) was 0.68 (SD = 0.10), Specific Source accuracy ($P_{\text{correct Specific Source response} | \text{Specific Source response made to old item}}$) was 0.70 (SD = 0.12), and both accuracy levels were significantly above chance (chance being

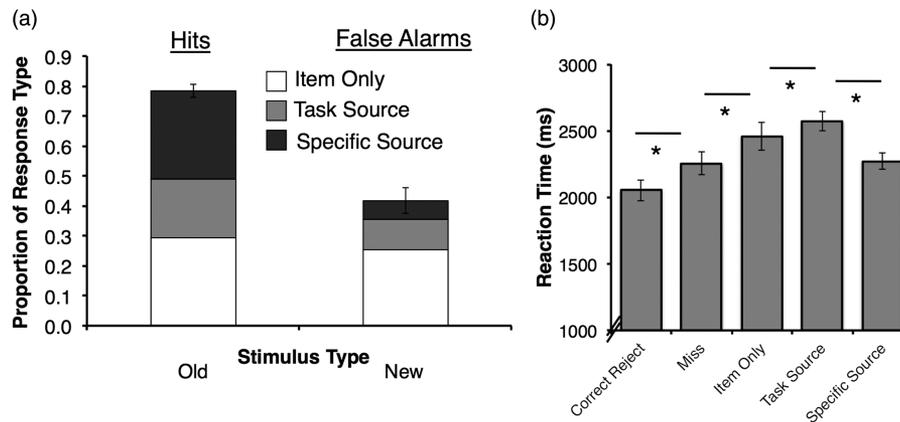


Figure 2. Behavioral performance. (a) Retrieval performance across response types. (b) Reaction time data varied significantly across conditions. all $*P < 0.05$; Error bars are standard error of the mean in (a) and standard error of the subject by condition interaction in (b).

0.5 for Task Source and 0.25 for Specific Source; all $t > 6.30$, all $P < 0.001$).

RTs varied according to retrieval outcome (all $F_{4,72} = 15.86$, all $P < 0.001$; Fig. 2b). Follow-up analyses revealed significant successive increases in RT from Correct Rejections to Misses to Item Only hits to Task Source hits. In addition, Specific Source hits were significantly faster than Task Source hits (see Supplementary Results for details). As detailed below, between-condition and between-trial differences in RT were used to characterize PPC functional responses during retrieval.

Attention Mapping Experiment

In the attention mapping experiment, participants performed a target detection task in which the size of the target was adjusted between runs to yield approximately 80% accuracy, thereby ensuring that the task was attentionally demanding (i.e., neither too difficult nor too simple to perform). Across participants, the average percentage of targets correctly detected was 80.2% (range: 75.5%–84.5%), and the false alarm rate was 2.1% (range: 0.8%–5.9%).

fMRI Analyses

With the aim of characterizing the fine-grained functional organization of PPC as it relates to memory and attention, our primary analyses proceeded in 3 steps. First, we conducted 4 contrasts in the memory experiment, each targeted to reveal a functionally distinct pattern of activation. Specifically, given prior observations in the memory literature of heterogeneity of functional subdivisions in PPC during retrieval, 2 contrasts were designed to reveal regions associated with the mnemonic processes of item recognition (familiarity) and recollection. Next, given recent findings concerning the role of attention during retrieval, a third contrast examined the relationship between retrieval activation and retrieval RT (a potential marker of top-down attention demands). Finally, motivated by a prior observation that right ventral PPC may demonstrate a “negative recollection effect” (Vilberg and Rugg 2007, 2008b), a fourth contrast was used to identify regions demonstrating greater activation during item memory compared with source recollection.

Second, to examine the full pattern of data across all retrieval conditions in each region and to test for functional dissociations between regions, we conducted ROI analyses on

regions identified in the 4 directed contrasts described above and then examined region by condition interactions for these ROIs. To accomplish this in a statistically unbiased fashion, we implemented a split-half approach, wherein the specified contrasts identified functional ROIs based on half the data (all $P < 0.001$, uncorrected; 5-voxel extent) that were then used for analysis of the other half of the data. This split-half procedure is a statistically independent approach that allowed us to 1) test for within-experiment replication of the voxel-level effects and 2) assess the full pattern of functional activation in ROIs across conditions, including functional dissociations between ROIs (see Methods section).

Finally, we used the independent attention mapping data to identify 7 topographically organized maps in each subject and then assessed the degree of functional overlap between posterior parietal memory and attention effects.

Graded Memory Experiment

Lateral IPS and successful item recognition. We first identified regions involved in the successful recognition of items (i.e., familiarity-based recognition) by comparing items correctly identified as old but without accompanying source memory (Item Only) to items correctly identified as novel (Correct Rejections). This contrast revealed significantly activated voxels in a number of parietal and frontal regions (Table 2), including left lateral IPS (spanning the anterior and mid-extent of the IPS), bilateral superior frontal sulcus (SFS), and SPL extending into precuneus (Fig. 3a).

To understand the full pattern of activity across all 5 memory conditions in these regions, we extracted the BOLD response for each memory condition from each Item Only > Correct Rejections ROI (IPS coordinates: $-30, -54, 39$; SPL/precuneus coordinates: $-12, -63, 60$; SFS coordinates: $-24, 6, 60$). Note that given the predominance of left-lateralized effects in PPC in the memory literature, our analyses were restricted to the left hemisphere. Again, to ensure statistical independence, split-half analyses were used to extract the percent signal change data from each ROI in an unbiased manner (see Methods section). These analyses revealed 2 qualitatively different patterns of effects, with lateral IPS showing one pattern and SPL/precuneus and SFS exhibiting a second, distinct pattern.

Table 2
Frontal and parietal regions modulated by retrieval outcome

Anatomical area	~BA	Hemisphere	x	y	z	Z Score	Size (mm ³)
Item Only > Correct Rejections							
Superior frontal sulcus/ superior frontal gyrus	6	L	-24	6	60	4.52	3429
		R	18	6	63	3.88	621
Cingulate sulcus/ superior frontal gyrus	32	L	-6	21	45	3.52	648
		R	-6	27	36	3.31	
		R	12	24	36	3.71	189
Middle frontal gyrus	9/46	L	-48	30	36	4.02	486
Middle frontal gyrus/ frontopolar cortex	10	L	-39	54	15	4.13	1539
		L	-30	48	9	3.53	
Intraparietal sulcus/ inferior parietal lobule	7/39/40	L	-30	-54	39	4.19	3807
		L	-48	-42	51	3.44	
		L	-45	-48	45	3.36	
Superior parietal lobule/ precuneus	7	L	-12	-66	45	4.05	3483
		L	-12	-63	60	3.93	
		R	15	-69	54	3.7	486
Task Source > Specific Source							
Superior frontal sulcus	6	L	-21	6	66	3.22	135
Middle frontal gyrus	9	R	33	36	30	3.61	270
Superior parietal lobule	7	L	-15	-66	54	3.69	810
		R	18	-66	51	4.03	891
Specific and Task Source > Item Only^a							
Middle frontal gyrus	8	L	-33	15	51	4.12	432
Inferior frontal sulcus	9/46	R	57	27	30	3.66	891
		R	57	21	36	3.65	
		R	60	15	27	3.43	
Superior medial gyrus	11	L	-3	33	-15	3.59	216
Transverse orbital sulcus	11	R	33	36	-9	3.44	216
Superior frontal gyrus	8/9	L	-9	54	42	4.45	10 098
		L	0	36	42	4.29	
		L	-12	39	48	4.03	
Postcentral gyrus/inferior parietal lobule	2/40	L	-36	-39	42	4.23	1944
		L	-45	-33	39	3.7	
		L	-42	-42	57	3.53	
Precuneus/posterior cingulate	7/23/30/31	L	-3	-57	27	5.29	18 279
		L	-3	-69	36	4.6	
		L	-3	-39	6	3.56	
Parietooccipital sulcus/ precuneus	7	L	-15	-69	27	3.45	162
Angular gyrus	39	R	42	-69	39	3.65	2916
		R	36	-66	57	3.41	
		R	36	-57	42	3.27	
		L	-39	-72	42	4.75	6777
		L	-42	-66	54	4.6	
		L	-39	-63	39	4.59	
Item Only > Specific and Task Source							
Superior frontal gyrus	6	R	15	15	66	4.11	675
Insula	13	L	-42	-9	0	3.85	405
Supramarginal gyrus	40	L	-66	-36	33	3.25	162
		R	63	-45	30	4.1	1350

Coordinates are in MNI space. BA, Brodmann's area; full set of nonfrontoparietal coordinates are available by request.

^aExclusively masked with Item Only > Correct Rejections at all $P < 0.1$.

In lateral IPS, there was a graded pattern of activity that varied with memory strength, such that both Task Source and Specific Source trials elicited greater activity than Item Only trials (both $t > 4.28$; $P < 0.001$), which in turn elicited greater activity than both Correct Rejections and Misses (both $t > 3.51$; $P < 0.005$) (Fig. 3*b*). This profile of activity is consistent with prior studies that have reported dorsal parietal BOLD activity that scales in a graded manner with memory strength or with the mnemonic process of familiarity (Yonelinas et al. 2005; Daselaar et al. 2006), assuming that trials on which some kind of source information is recalled are also associated with stronger familiarity, relative to Item Only trials. In contrast, the SPL/precuneus and SFS ROIs that were defined from this same voxelwise contrast (Item Only>Correct Rejections) had a qualitatively different overall pattern: 1) Task

Source trials elicited greater activity than Specific Source trials [significant difference in SFS (all $t_{18} = 3.87$; all $P < 0.005$) and a trend in SPL (all $t_{18} = 1.83$; all $P < 0.1$), and 2) Specific Source activity did not differ from Item Only activity in either SFS or SPL (all $t < 0.5$; all $P > 0.6$). These findings suggest that left IPS, but not SPL, tracks gradations in memory strength.

SFS and SPL are functionally distinct from lateral IPS. The difference between Task and Specific Source conditions observed in the SFS and SPL ROIs is not likely to index differences in either familiarity or recollection, given that a region that tracks familiarity or recollection would be unlikely to show *greater* activity for items that were remembered with *less* contextual information (Task Source) compared with items that were remembered with more contextual information (Specific Source). On the other hand, the locations of these ROIs and their activity profiles are broadly compatible with effects stemming from graded differences in the engagement of top-down attention during retrieval. First, both regions roughly overlap with the dorsal frontal-parietal top-down attention network (e.g., Shulman et al. 2003) reported MNI coordinates of -19, -61, 51 [SPL] and -27, -9, 53 [dorsal frontal], compared with coordinates here of -12, -63, 60 [SPL] and -24, 6, 60 [SFS]). Second, the direction of activation (Task > Specific Source) mirrored the corresponding condition-level differences in RT, as Task Source trials were associated with RTs that were on average 335 ms slower than those on Specific Source trials (Fig. 2*b*). Motivated by these observations, we conducted 2 follow-up analyses: the first was a voxelwise contrast to identify regions that were more active during Task Source than Specific Source trials, and the second formally tested whether the resulting ROIs parametrically tracked RT on a trial-by-trial basis.

Voxelwise comparison of Task Source > Specific Source revealed a number of clusters, including significant effects in left superior frontal cortex and bilateral SPL/precuneus (Fig. 3*c*). These regions overlapped with those observed in the Item Only > Correct Rejections contrast (compare with Fig. 3*a*). Statistically independent ROI analyses on percent signal change in left SPL (coordinates: -15, -66, 54; Fig. 3*d*) replicated the voxelwise Task Source > Specific Source difference (all $t_{18} = 2.59$; all $P < 0.05$) and also confirmed that left SPL shows an Item Only > Correct Rejections effect (all $t_{18} = 2.13$; all $P < 0.05$). Importantly, an ROI \times Condition interaction revealed that the SPL activity profile differed from that of the lateral IPS region that exhibited memory strength effects (all $F_{4,72} = 4.94$, all $P < 0.005$), indicating that SPL/precuneus and lateral IPS support distinct processes during episodic retrieval. The SFS ROI (coordinates: -21, 6, 66) exhibited a pattern of activity similar to that in SPL and also significantly differed from the pattern of activity in lateral IPS (ROI \times Condition: all $F_{4,72} = 10.42$, all $P < 0.001$).

The rank order of response amplitude in left SPL [Task Source > (Specific Source, Item Only) > (Correct Rejections, Misses)] qualitatively resembled the rank order of between-condition RT differences. To more formally test the relationship between behavioral RT measures and PPC retrieval response amplitudes, we performed a parametric modulation analysis of the BOLD response based on within-condition trial-by-trial differences in RT. Regions exhibiting such a parametric modulation are those that demonstrate greater activity during more effortful trials (as indexed by longer RTs). This

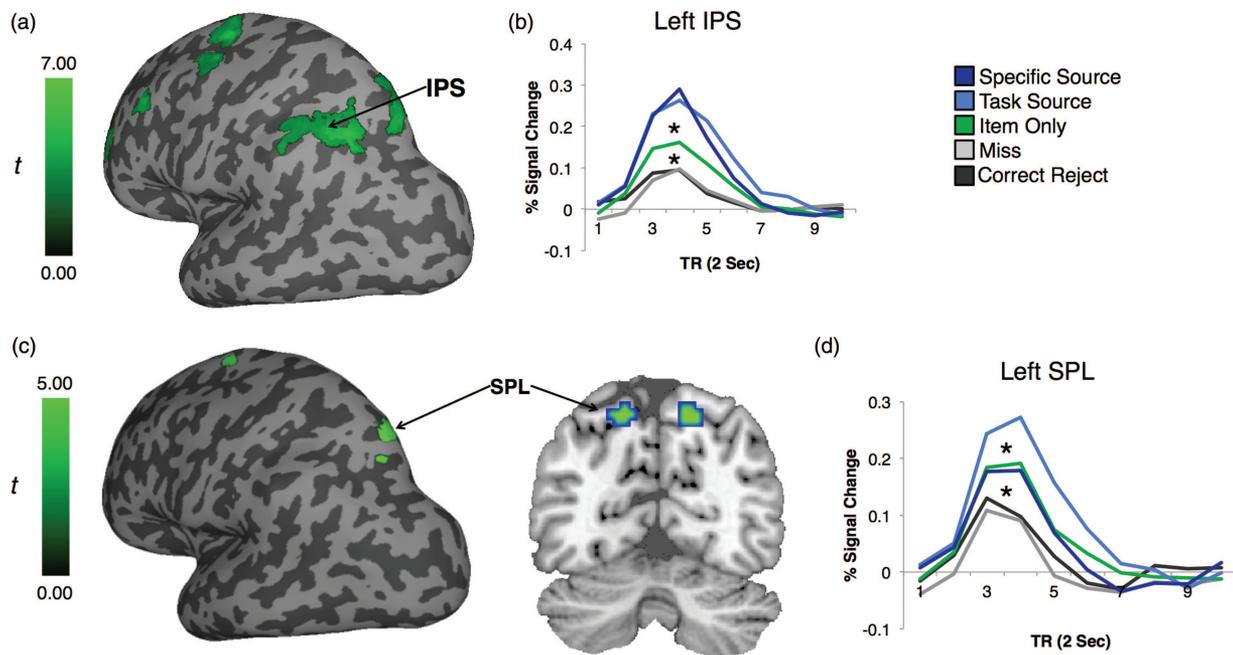


Figure 3. Functional heterogeneity of memory retrieval effects within dorsal PPC. (a) Voxelwise comparison of Item Only hits > Correct Rejections, thresholded at all $P < 0.001$, revealed a cluster of activity along the left intraparietal sulcus (IPS). (b) BOLD response amplitude in the left IPS ROI varied with memory strength. (c) Voxelwise comparison of Task Source > Specific Source, thresholded at all $P < 0.001$, revealed activity in the superior parietal lobule (SPL). (d) BOLD response amplitude in the left SPL ROI varied across the retrieval conditions, demonstrating a qualitatively different pattern from that in left IPS. All $*P < 0.05$.

analysis revealed that activity in the left SPL ROI showed significant positive modulation by RT in 4 of the 5 retrieval conditions (i.e., greater activity on trials with longer RT; β for the parametric modulation regressors were significantly greater than zero for Correct Rejections, Misses, Item Only, and Specific Source, all $t > 2.14$, all $P < 0.05$; but not for Task Source, all $t_{18} = 0.42$, all $P = 0.68$). None of the other parietal ROIs in this experiment displayed significant modulation by RT in multiple conditions.

Angular gyrus and graded recollection. We next sought to identify regions selectively sensitive to the recollection of source details by contrasting the Task Source and Specific Source conditions with the Item Only condition (i.e., Task Source and Specific Source > Item Only). To exclude voxels that showed item recognition effects, we exclusively masked the foregoing contrast with the results of the Item Only > Correct Rejections comparison described above (all $P < 0.1$, uncorrected). That is, we masked the primary contrast to restrict the ROI to those voxels that were selectively sensitive to recollection (Vilberg and Rugg 2007). The resulting contrast map revealed voxels in bilateral AnG and precuneus (Fig. 4a; see Supplementary Fig. S1) that were sensitive to source recollection but did not show item recognition effects even at a very lenient threshold (Table 2). Statistically independent analyses of percent signal change from the left AnG ROI (coordinates: $-39, -72, 42$) confirmed that there was significantly greater activation for both source conditions (Task and Specific) relative to Item Only (Fig. 4b; both all $t > 2.75$; all $P < 0.05$). Consistent with a recollection-sensitive mechanism (Vilberg and Rugg 2007, 2008a, 2009), this ROI also demonstrated greater activation during Specific Source compared with Task Source trials (all $t_{18} = 2.27$; all $P < 0.05$). Moreover, responses for Correct Rejections and Misses were significantly below baseline (t -test

vs. 0: all $P < 0.005$), extending prior observations using the remember/know procedure (Wheeler and Buckner, 2004; also see Nelson et al. 2010). The present data additionally revealed a trend for below baseline activity for Item Only trials (all $t_{18} = 1.95$; all $P = 0.067$), whereas activity for Specific Source trials was significantly above baseline (all $t_{18} = 2.68$; all $P < 0.05$).

Qualitatively, the pattern in left AnG was distinct from that in left IPS and from that in left SPL. Formally, interaction analyses confirmed that left AnG exhibited a pattern of activity across retrieval conditions that was significantly different from that in the IPS ROI that exhibited memory strength effects (ROI \times Condition: all $F_{4,72} = 2.72$, all $P < 0.05$), as well as from that in the SPL ROI that displayed RT-related effects (ROI \times Condition: all $F_{4,72} = 5.12$, all $P < 0.005$). Collectively, these analyses provide strong evidence for 3 functionally distinct retrieval-related patterns of responses in left lateral PPC.

Distinct memory-related effect in temporoparietal junction. As described above, activity in AnG within ventral PPC was associated with recollection. Based on a prior intriguing observation of a potential negative recollection effect that was located in or near right temporoparietal junction (TPJ; Vilberg and Rugg 2007, 2008b), we performed the reverse contrast (i.e., Item Only > Task and Specific Source) to assess whether TPJ shows a functionally distinct pattern from AnG. Strikingly, this voxelwise contrast revealed bilateral activation of TPJ (Fig. 4c and Table 2). Interestingly, as in studies of bottom-up attention, the extent of the effects was greater in the right than in the left TPJ (Corbetta et al. 2008). We therefore conducted statistically independent analyses of percent signal change in a right TPJ ROI (coordinates: $63, -45, 30$; Fig. 4d, right) and confirmed the Item Only > Task Source (all $t_{18} = 4.77$; all $P < 0.001$) and Item Only > Specific Source (all $t_{18} = 3.23$; all

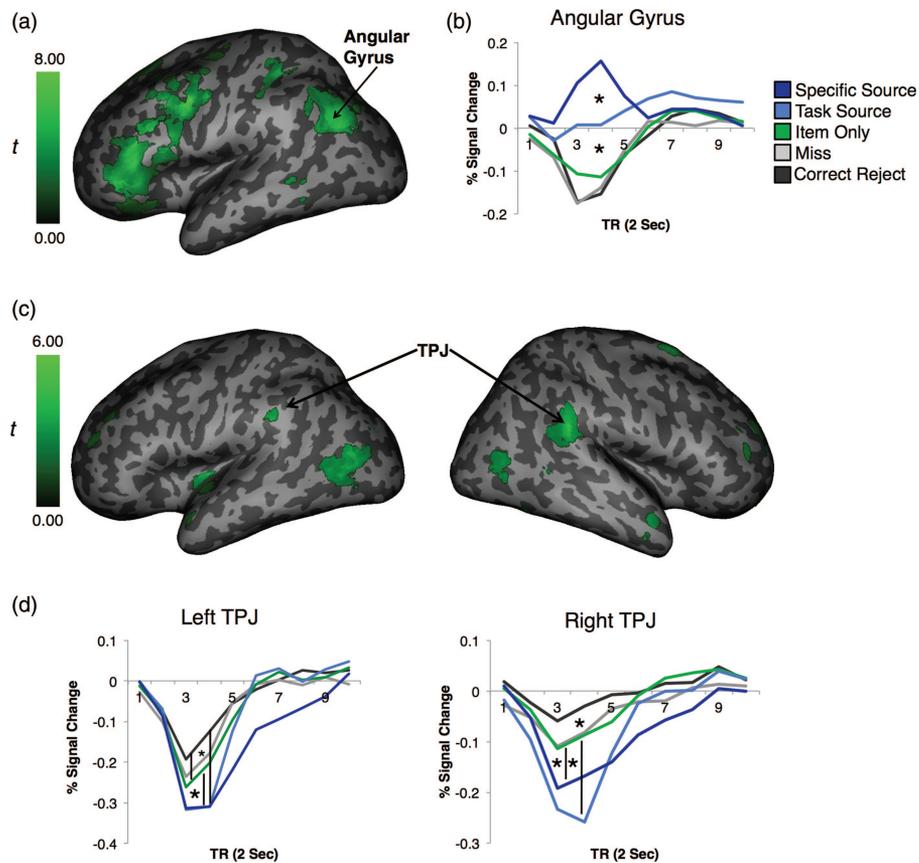


Figure 4. Functional heterogeneity within ventral PPC. (a) Comparison of (Task and Specific Source) > Item Only, thresholded at all $P < 0.001$ and exclusively masked with Item Only > Correct Rejections (all $P < 0.1$), revealed regions sensitive to recollection (also see Supplementary Fig. S1 for right hemisphere activations). (b) BOLD responses from an ROI in left angular gyrus varied as a function of the specificity of recollected information. (c) Voxelwise comparison of Item Only > (Task and Specific Source) revealed regions bilaterally within ventral PPC (data shown at all $P < 0.005$ for visualization purposes only). (d) ROI analysis revealed that activation in right temporoparietal junction (TPJ) qualitatively differed from that in angular gyrus and that activity in left TPJ was qualitatively similar to that in right TPJ. all $*P < 0.05$.

$P < 0.005$) differences. Additionally, Correct Rejections were significantly greater than Misses (all $t_{18} = 2.26$; all $P < 0.05$), and both Correct Rejections and Misses were significantly greater than both Task Source and Specific Source (all $P < 0.005$). The left TPJ ROI (coordinates: $-66, -36, 33$) displayed a similar pattern of activity to that of the right TPJ (ROI \times Condition interaction, all $F_{4,72} = 1.13$, all $P > 0.3$, Fig. 4d, left), with Item Only > Specific Source (all $t_{18} = 3.23$; all $P < 0.005$), Correct Rejections and Misses greater than both Task Source and Specific Source (all $P < 0.05$) and Correct Rejections greater than Item Only ($t_{18} = 2.20$; $P < 0.05$). Importantly, both left and right TPJ ROIs displayed distinct patterns of activity from the left AnG ROI that was associated with source recollection (ROI \times Condition interaction, right: all $F_{4,72} = 23.58$, all $P < 0.001$; left: all $F_{4,72} = 17.75$, all $P < 0.001$), demonstrating that anterior and posterior portions of ventral PPC perform different operations during episodic retrieval. Moreover, both left and right TPJ displayed distinct patterns of activity from the aforementioned left SPL and left IPS ROIs (pairwise ROI \times condition interactions: all $F > 15$; all $P < 0.001$). We consider possible functional interpretations of TPJ activation in the Discussion.

Taken together, these results demonstrate robust functional heterogeneity in left PPC during retrieval, as demonstrated by both voxelwise comparisons and the statistically independent ROI analyses (ROI \times Condition interaction for all 4 left PPC ROIs: all $F_{12,72} = 13.08$, all $P < 0.001$). Although several other

studies have described functional parcellations of PPC during retrieval (Nelson et al. 2010; Sestieri et al. 2010, 2011), this is the first evidence that a quadruple functional dissociation can be observed for a single episodic memory task.

Attention Mapping Experiment

To examine the relationship between attention-related and memory-related responses in dorsal PPC, we conducted a spatial attention mapping procedure on a subset of the participants from the memory experiment. Specifically, participants performed an attention-demanding mapping task known to evoke spatially selective responses in topographically organized regions along the IPS and SPL. We identified 7 of these spatial attention maps (conventionally labeled IPS0-5 and SPL1; Fig. 5a) in each participant's left hemisphere (the hemisphere of interest, given that retrieval-related effects were found in left PPC in both the present study and the majority of studies in the literature (Wagner et al. 2005; Cabeza et al. 2008; Vilberg and Rugg 2008b)). The attention maps were then assessed within-subject with respect to 1) their anatomical relationships to memory-related effects in the graded memory experiment, and 2) their response profiles across retrieval conditions during the graded memory experiment.

Anatomical relationships among regions associated with episodic retrieval effects and topographic maps of spatial attention in PPC. We first examined the overlap of PPC

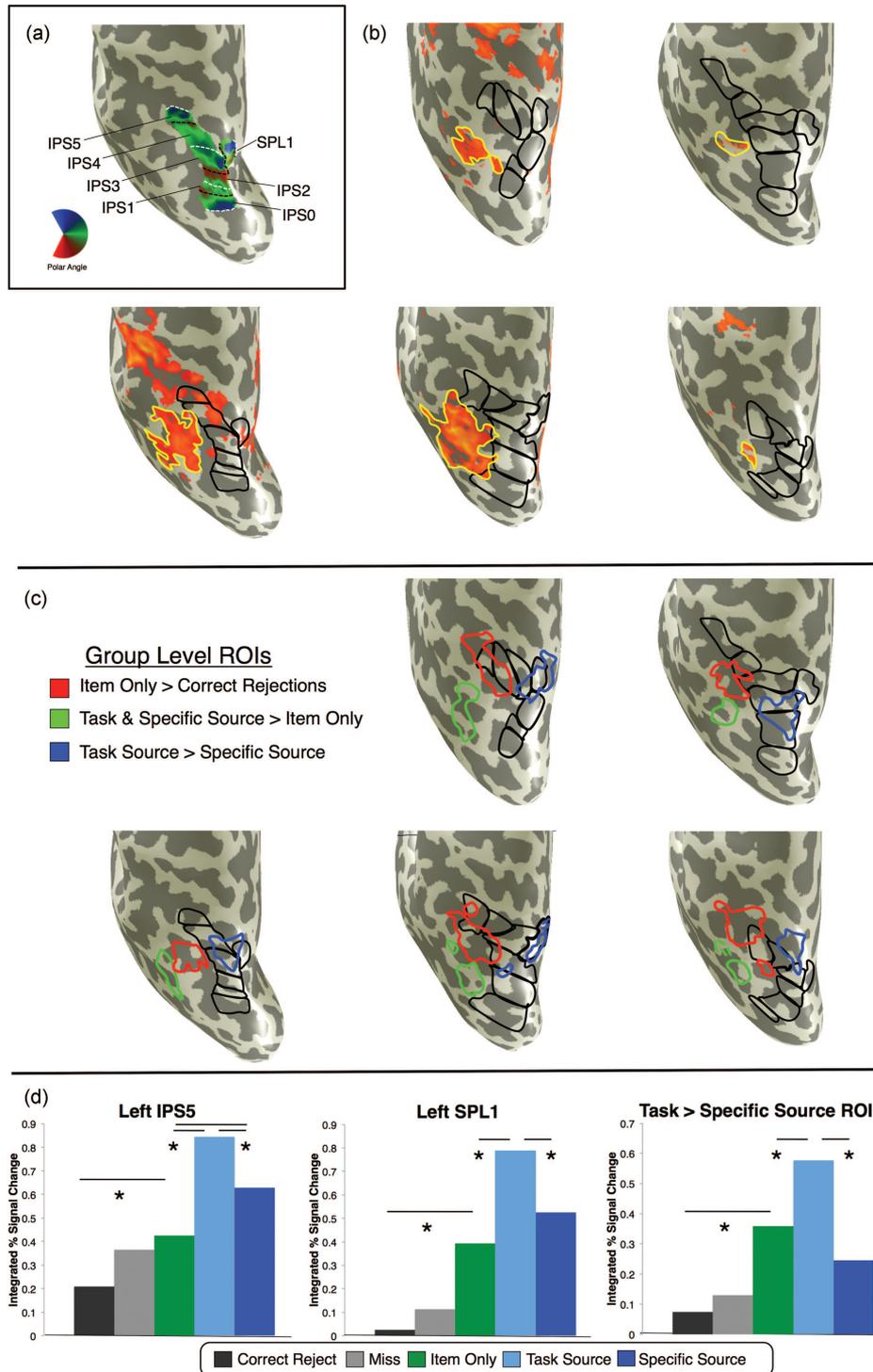


Figure 5. Relationship between memory-related effects and topographic visual field maps in PPC. Dorsal view of (a) response phases in a representative subject (color wheel indicates locations in contralateral visual space; dotted lines indicate phase reversals/field map boundaries corresponding to representations of the upper or lower vertical meridian in the visual field). Five participants' left hemispheres with (b) regions significantly activated by Specific Source > Item Only (all $P < 0.001$) in orange (consistently lateral to the topographically organized maps), and (c) reverse-normalized group-level ROIs superimposed. In both (b) and (c), visual field maps for each subject are outlined in black. (d) BOLD responses for topographically defined IPS5 (left), SPL1 (middle), and for the group-level ROI defined from Task > Specific Source in the memory study (right; all $*P < 0.05$ using bootstrap analysis, see text). Also see Supplementary Figure S2 for memory-related BOLD responses in IPS0 and IPS4.

attention maps IPS0-5 and SPL1 with memory-related effects using 1) a voxelwise contrast of memory-related effects at the individual-subject level, and 2) the group-level ROIs identified in the memory experiment, rendered on each participant's cortical surface.

In the first analysis, we sought to identify regions that were sensitive to both item memory strength and recollection but did not track retrieval RT (under the assumption that activity correlated with RT may reflect the engagement of attention during retrieval). To do so, we identified voxels with larger

responses on Specific Source than on Item Only trials, because both recollection and item memory were likely stronger on Specific Source trials and, on average, Specific Source trials were associated with faster RTs than Item Only trials. Clusters of significant activity for this contrast were found in PPC in every participant (all $P < 0.001$, uncorrected) and localized lateral to the attention-mapped IPS0-5 and SPL1 regions (Fig. 5b).

Second, we rendered 3 of the group-level memory ROIs identified in the memory experiment (left IPS, SPL, and AnG; TPJ was not included given its large anatomical distance from dorsal PPC) onto each participant's cortical surface to assess the anatomical overlap between these memory-sensitive regions and the PPC spatial attention maps (Fig. 5c). In all 5 participants, the AnG ROI that tracked recollection (defined by Task and Specific Source > Item Only) was lateral to the spatial attention maps and did not overlap with any of them. The IPS ROI that tracked memory strength (defined by Item Only > Correct Rejections) typically was located on the fundus/lateral bank of the IPS and was lateral to the spatial attention maps in 4 of 5 participants. In contrast, the SPL ROI that demonstrated RT-related retrieval activation (defined by Task Source > Specific Source) substantially overlapped with the spatial attention maps in 4 of 5 participants. Additionally, the percentage of the area of each memory ROI that overlapped with any of the attention maps was greater for the SPL (48.1%) than for the IPS (12.4%; t -test vs. SPL: all $t_4 = 3.09$; all $P < 0.05$) or the AnG (0%; t -test vs. SPL: all $t_4 = 4.05$; all $P < 0.05$) memory ROIs.

The anatomical correspondence between the memory-defined SPL ROI and topographically organized PPC regions provides additional evidence for a role of this RT-sensitive SPL region in top-down attention. To quantify attention signals within the memory-defined SPL, IPS, and AnG ROIs, we computed mean coherence (BOLD fluctuations at the frequency of the rotating wedge stimulus normalized by the amplitude of the fluctuations at all frequencies in the time series; see Methods section). This measure of spatially selective responses reflects a combination of attention and visually evoked signals and provides a metric for comparing the strength of spatially specific signals recorded during the attention mapping in the 3 memory-defined ROIs. The memory-defined SPL ROI that tracked retrieval RT displayed significantly greater coherence during the attention task (0.34) relative to the IPS ROI that tracked memory strength (0.21, all $t_4 = 5.20$, all $P < 0.01$) and relative to the AnG ROI that tracked recollection (0.25, all $t_4 = 2.79$, all $P < 0.05$), consistent with the pattern of spatial overlap between the memory-defined ROIs and the topographic maps of attention. While the IPS and AnG ROIs displayed above-threshold coherence values, it is worth noting that they failed to exhibit systematic topographic visual field organization (suggesting the presence of voxels that either have a receptive field or contain noise with power at the stimulus frequency). Whereas, as noted above, the SPL ROI consistently overlapped with regions containing continuous maps of visual field locations along the cortical surface.

Response profiles of IPS0-5 and SPL1 during episodic retrieval. To determine which of the topographic attention maps showed memory-related effects, we conducted a bootstrapped one-way ANOVA analysis (see Methods section)

on BOLD response amplitudes from the memory experiment in left IPS0-5 and SPL1, with memory condition as the critical factor. A significant effect of condition was found in IPS0, IPS4, and IPS5 (all $P < 0.05$), with a trend in SPL1 (all $P = 0.087$). Subsequent bootstrap analyses tested whether there were significant pairwise differences in each of these ROIs for the 4 primary comparisons of interest: Item Only vs. Correct Rejections, Task Source vs. Specific Source, Task Source vs. Item Only, and Specific Source vs. Item Only.

Left topographic IPS5 and SPL1 displayed similar patterns of activity across conditions (ROI \times Condition interaction, all $P > 0.9$; note: the functional pattern in SPL1 should be interpreted with caution, given that there was only a trend-level effect of memory condition in the ANOVA for this ROI). In both IPS5 and SPL1, response amplitude was greater for Task Source than for Specific Source (all $P < 0.05$), greater for Task Source than for Item Only (all $P < 0.001$), and greater for Item Only than for Correct Rejections (all $P < 0.01$; Fig. 5d). Additionally, Specific Source was greater than Item Only in IPS5 (all $P < 0.05$). These patterns of memory effects in IPS5 and SPL1 were very similar to the pattern of activity in the memory-defined SPL ROI across all participants (Fig. 3d), as well as in the subset of participants in the attention mapping experiment (Fig. 5d, right).

In left IPS4, the pattern of activity across memory conditions did not significantly differ from that in left SPL1 and left IPS5 (see Supplementary Fig. S2; ROI \times condition interactions, all $P > 0.4$). In this region, Task Source was greater than Item Only (all $P < 0.01$), as was Specific Source (all $P < 0.05$). However, in contrast to IPS5 and SPL1, there were no significant differences between Item Only and Correct Rejections or between Task and Specific Source (all $P > 0.2$). The absence of these differences, which could reflect low statistical power, limits interpretation at this time regarding how the functional profile of IPS4 resembles the functional profile of any of the memory-defined ROIs.

Finally, the pattern in left IPS0 significantly differed from that in IPS4, IPS5, and SPL1 (see Supplementary Fig. S2; ROI \times condition interactions with IPS4, IPS5, and SPL1, all $P < 0.05$). In contrast to these other regions, IPS0 qualitatively demonstrated a U-shaped function across memory strength. The bootstrap analysis revealed significant differences between Correct Rejections and Item Only (all $P < 0.001$) and between Specific Source and Task Source (all $P < 0.05$). Interestingly, IPS0 was also the only attention map that did not overlap with any of the memory ROIs in any subject.

Collectively, these findings indicate that 1) dorsal PPC topographic maps of attention exhibit different patterns of activity across episodic retrieval conditions, and 2) the pattern of retrieval responses in topographic areas IPS5 and SPL1 resemble that observed in the SPL region that tracked RT in the memory experiment. The latter observation supports the interpretation that activation in SPL during episodic retrieval reflects the engagement of top-down visuospatial attention, particularly when retrieval decisions are effortful and/or uncertain.

Discussion

This study provides evidence that PPC contributions to episodic retrieval cannot be adequately described by current coarse, 2-process descriptions. Our experiments reveal rich functional heterogeneity in PPC, with SPL appearing to track

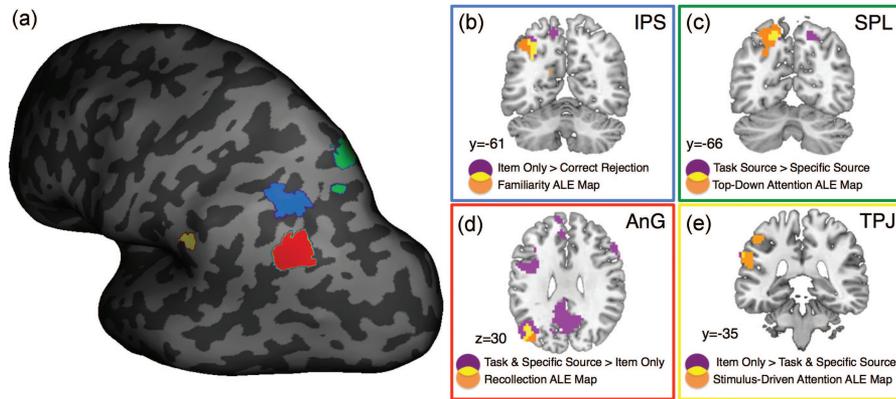


Figure 6. Formal meta-analysis of spatial relationships between the present findings and the literature. (a) Locations of the 4 functionally distinct ROIs from the group-level memory analysis (IPS: blue, SPL: green, AnG: red, TPJ: yellow). (b, c, and e) Coronal and (d) axial views of the 4 group-level contrasts from the memory experiment (thresholded at all $P < 0.001$, purple) and Activation Likelihood Estimation (ALE) maps (Eickhoff et al. 2009) of relevant studies in the memory and attention literatures (thresholded with a FDR of all $P < 0.05$, orange; overlap rendered in yellow). Comparison of the findings in the current study to those reported in the literature reveals overlap between (b) the IPS region displaying memory strength effects here and the IPS region consistently associated with familiarity across studies of episodic retrieval (as compiled in Vilberg and Rugg 2008b), (c) the SPL region positively tracking retrieval reaction time here and the SPL region that is consistently associated with top-down attention across studies of attention (as compiled in Hutchinson et al. 2009), (d) the AnG region displaying successful recollection effects here and the AnG region consistently associated with recollection across studies of episodic retrieval (as compiled in Vilberg and Rugg 2008b), and (e) the left TPJ region displaying greater activity for Item Only than for Task and Specific Source trials here and the TPJ region consistently associated with the stimulus-driven reflexive orienting of attention across studies of attention (as compiled in Hutchinson et al. 2009). Note that only left parietal peak-voxel coordinates were used in the generation of the ALE maps, whereas the bootstrapped null distribution to which they were compared necessarily included voxels throughout the brain (Eickhoff et al. 2009). This slightly lowered the resulting P values (and consequently produced more liberal estimates of activation in the ALE maps).

demands on top-down attention during retrieval and spatial attention tasks, whereas retrieval-related responses in other PPC substructures (lateral IPS, AnG, and TPJ) require alternative accounts. In particular, the graded memory task revealed 4 functionally distinct PPC subregions (Fig. 6a): 1) a region along the fundus and lateral bank of the IPS exhibited responses that scaled with the degree of memory strength; 2) a region in the SPL tracked the time required to reach a memory decision, rather than mnemonic strength, likely reflecting differential demands on top-down attention; 3) a region of AnG displayed graded activity that varied with the specificity of recollected event (source) details; and 4) a region in TPJ demonstrated activity that varied with memory outcome in a manner that was distinct from the other regions. Critically, at the individual-subject level, PPC subregions tracking memory strength and recollection were largely distinct from parietal areas that represent the location of top-down spatial attention. Specifically, topographic maps of spatial attention along the IPS/SPL were medial to the IPS and AnG regions that exhibited memory strength and recollection-related effects, whereas patterns of activity in a subset of these maps (IPS5 and SPL1) were similar to those observed in SPL during episodic retrieval.

Functional Heterogeneity in PPC

Taken together, our results indicate that parietal contributions to episodic retrieval are not fully described by only 2 mechanisms that are centered on dorsal and ventral PPC (Wheeler and Buckner 2004; Wagner et al. 2005; Cabeza 2008; Cabeza et al. 2008; Ciaramelli et al. 2008; Vilberg and Rugg 2008b). Rather, at least 4 distinct components play dissociable roles in memory decisions. The quadruple functional dissociation revealed in the present study extends recent meta-analytic (Hutchinson et al. 2009) and within-study (Sestieri et al. 2010, 2011) evidence that attention-related operations are associated with regions beyond lateral IPS and AnG, which track

gradations in memory strength and event recollection, respectively. The regions delineated here are also in agreement with a proposed parcellation of left PPC based on a combination of task-evoked (episodic retrieval) and resting state data (Nelson et al. 2010; also see Sestieri et al. 2011). The current results provide key conceptual extensions to this delineation by 1) providing information regarding how topographically organized attention-related regions of PPC spatially relate to regions associated with core mnemonic processes of item memory strength and recollection, and 2) characterizing how regions involved in attention are systematically engaged during episodic retrieval. Below, we discuss differential retrieval effects in dorsal (SPL vs. lateral IPS) and ventral (TPJ vs. AnG) PPC.

Dorsal PPC: Lateral IPS versus SPL

Our results provide compelling evidence for a functional distinction within dorsal PPC, with the lateral extent of IPS showing a pattern of responses that is dissociable from that in SPL. In particular, although both IPS and SPL displayed greater activity for hits than for correct rejections—consistent with numerous prior findings broadly implicating dorsal PPC in item recognition—the full pattern of retrieval-related activity revealed distinct response profiles in the 2 regions. Specifically, the IPS region exhibited activity consistent with a mechanism that tracks perceived memory strength (or item familiarity, assuming that trials on which the source was recollected were also associated with higher perceived familiarity relative to Item Only trials). Figure 6b illustrates the anatomical convergence between the locations of the memory strength effect in IPS in the present study and an IPS region that formal meta-analysis revealed to be consistently associated with familiarity-based recognition (Vilberg and Rugg 2008b; Uncapher et al. 2010).

One possibility is that, during recognition memory decisions, lateral IPS serves as a “mnemonic accumulator” of signals

from the medial temporal lobe to facilitate memory-guided action selection (Wagner et al. 2005; Donaldson et al. 2010, cf. Guerin and Miller 2011). This interpretation is supported by prior research suggesting that IPS activity during perceptual decisions in humans (Ploran et al. 2007; Heekeren et al. 2008; Tosoni et al. 2008; Kayser et al. 2010; Ploran et al. 2011, cf. Ho et al. 2009; Guerin and Miller 2011) and lateral intraparietal activity in nonhuman primates (Shadlen and Newsome 1996, 2001; Schall 2003; Kiani et al. 2008; Kiani and Shadlen 2009) is associated with the accumulation of evidence to guide perceptual decision making. In the present study, mnemonic evidence was objectively measured with source recollection and item recognition outcomes. While this yielded multiple conditions that differed in memory strength, future studies that measure memory strength as a continuous factor that varies on a trial-by-trial basis may provide a more direct test of the accumulator account of lateral IPS activity during retrieval. Moreover, such studies may help to resolve a challenge for the accumulator account—the absence of a relationship between RT and IPS activity in the present study.

Regardless of the exact mechanistic underpinnings of the lateral IPS memory strength effect, the present data reveal that the region is functionally and anatomically distinct from a more medial and superior region in SPL. In particular, rather than tracking memory strength, SPL showed greater activity on more uncertain retrieval trials (i.e., those associated with longer RTs). A positive correlation between RT and activity in SPL on individual trials was significant in 4 of 5 retrieval conditions in the present dataset, and the same ROI produced a significant correlation with RT in a subsequent experiment (Hutchinson et al. 2010), providing evidence that the relationship is reliable. A positive relationship between RT and dorsal PPC activity has been reported across a wide variety of tasks (Honey et al. 2000; Binder, Medler et al. 2005; Binder, Westbury et al. 2005; Yarkoni et al. 2009), and previous memory retrieval studies have revealed greater SPL activity during low confidence relative to high confidence recognition decisions (reviewed in Cabeza et al. 2008).

One account of the pattern of SPL activity in the present study is that it reflects greater demands on top-down attention during retrieval decisions associated with uncertainty. This account is supported by 3 further observations. First, the present SPL region that tracks RT anatomically overlaps with an SPL region that formal meta-analysis revealed to be a component of the putative top-down attention network described by Corbetta and Shulman (2002) (Fig. 6c). Second, a subset of topographic regions defined in our top-down spatial attention mapping procedure (IPS5 and SPL1) displayed a pattern of retrieval activity that was qualitatively similar to that in the SPL region identified in the memory task. Finally, part of this functional similarity may reflect the fact that the SPL region identified in the memory task anatomically overlapped with topographically organized attention maps in individual subjects (Fig. 5c), providing direct evidence that the SPL region that tracks retrieval RT corresponds to parietal areas that subserve top-down visuospatial attention.

Although the above evidence suggests SPL is related to the deployment of top-down attention, the precise attentional process engaged during memory retrieval is less clear. Given the nature of the present retrieval task, including its response selection demands, multiple distinct types of attention may have been engaged. One possibility is that SPL mediates

top-down attention to the retrieval cues themselves (i.e., the word cues), while another is that attention is directed to the products of retrieval (i.e., attention to internally generated representations). From the latter perspective, conditions and trials associated with longer RTs may reflect sustained allocation of attention to memory signals in the service of memory-guided decisions (i.e., SPL activation increases with decision uncertainty that is associated with increased attention to mnemonic evidence). The fact that the SPL region identified in the retrieval task overlapped with some of the topographic attention maps is consistent with the interpretation that SPL-mediated visuospatial attention is allocated to spatial aspects of the retrieval cues, because there is no a priori reason to predict that, in the present paradigm, attention to retrieved information would engage visuospatial computations. Yet another possibility is that the type of attention engaged during retrieval relates to the response selection demands of the task, rather than to attention to retrieval cues or to memory signals per se. In particular, given the complex response mapping required for the task (8 response options), it is possible that the correlation between SPL activity and RT reflects increased top-down attention in the service of maintaining and selecting stimulus-response mappings. Again, this account must also accommodate the substantial amount of overlap of the SPL ROI with cortex that codes information about visual field locations (e.g., perhaps the stimulus-response mappings were spatially represented). Although further research is needed to adjudicate among these interpretations, the current results suggest that attention-based accounts of SPL retrieval activity should consider possible contributions of visuospatial processing.

The current study also provides novel evidence regarding the functional properties of topographically mapped PPC regions. Just as recent studies in visual (Brewer et al. 2005; Larsson and Heeger 2006; Sayres and Grill-Spector 2008; Arcaro et al. 2009; Kolster et al. 2010; Weiner and Grill-Spector 2010, 2011; Rauschecker et al. 2011), frontal (Hagler and Sereno 2006; Kastner et al. 2007), and parietal cortex (Levy et al. 2007; Swisher et al. 2007) illustrate the benefit of multiple experimental techniques for clarifying the complexity of neural organization in both topographic and nontopographic areas, the present study demonstrates the generalizability of this approach to regions involved in multiple aspects of memory and attention. In particular, our results reveal heterogeneity across topographically organized PPC subregions, with 1) IPS0 displaying a distinct pattern of activity from IPS4, IPS5, and SPL1, and 2) IPS1-3 not exhibiting differential responses across retrieval conditions (though future studies with additional power are required to draw definitive conclusions about the relative effects of retrieval outcomes on responses in these areas). Thus, while IPS and SPL regions have been associated with top-down spatial attention in prior work (Tootell et al. 1998; Silver et al. 2005; Konen and Kastner 2008a; Silver and Kastner 2009, but see SPL1 in Szczepanski et al. 2010), the observation of heterogeneity here is broadly consistent with increasing evidence for a diversity of functions across topographically organized parietal maps (Konen and Kastner 2008a, 2008b; Sheremata et al. 2010). Given that we did not record eye movements, another possible source of functional heterogeneity is that eye movements during retrieval might have differentially affected fMRI responses (Konen and Kastner 2008a). Understanding the distinct contributions

of parietal subdivisions to complex cognitive processes is a promising direction for future research.

As just noted, a potential limitation of the current study is the absence of eye position measurements during the attention task. Specifically, it is possible that small eye movements towards the target produced slight underestimations of the extent of the topographic maps in PPC. Importantly, Swisher et al. (2007) found that the foveal representation is on the lateral side of these areas and the contralateral peripheral representation is on the medial side. Given that the memory-related activity observed in the present study was always lateral to or overlapping with the IPS areas, any underestimation of the peripheral extent of the IPS areas due to imperfect fixation during attention mapping cannot account for those cases in which there was no overlap between the topographic attention areas and the memory-related activity. It is also worth noting that although the current study had a relatively small sample size ($N=5$) for the attention mapping experiment, this sample size is comparable to those used in prior topographic mapping studies of these areas (e.g., Silver et al. 2005; Konen and Kastner 2008a, 2008b). Critically, our within-subject experimental design controlled for many sources of variance, thereby facilitating comparisons between memory-related and attention-related patterns of responses. Nevertheless, it is possible that future studies that employ larger samples sizes will reveal additional memory-related functional distinctions that were not detected in the present study.

Ventral PPC: AnG versus TPJ

Within ventral PPC, AnG and TPJ differed substantially in their response characteristics, providing compelling empirical support for the recent proposal that ventral PPC cannot be considered a single functional unit during episodic retrieval (Hutchinson et al. 2009). In particular, response amplitude in left AnG parametrically varied with the specificity of source recollection (Specific Source > Task Source > Item Only) and did not significantly differ for Item Only, Miss, and Correct Rejection trials. The location of this recollection effect overlaps with an AnG region that formal meta-analysis revealed to be consistently associated with recollection (Fig. 6d). Insofar as the specificity of the source memory judgment reflects the amount of information retrieved from episodic memory, the current results complement prior empirical findings showing graded recollection effects in AnG and nearby regions (Vilberg and Rugg 2007, 2008a, 2009). At a mechanistic level, the results are consistent with theoretical accounts of AnG as being an “output buffer” for episodic information (Baddeley 2000; Wagner et al. 2005; Vilberg and Rugg 2008b) or a “convergence zone” that relationally binds reinstated event features (Shimamura 2011). While future studies are required to adjudicate between these 2 hypotheses of AnG function during episodic remembering, the present data indicate that activity in AnG positively tracks event recollection, a pattern that unambiguously distinguishes it from TPJ.

Indeed, response amplitude in TPJ did not positively correlate with either item memory strength or the level of source recollection. Instead, TPJ exhibited deactivations that qualitatively tracked between-condition differences in RTs, with the largest deactivation for the condition with the longest RTs (Task Source) and the smallest for the condition with the shortest RTs (Correct Rejections). Thus, the pattern of activity in TPJ qualitatively resembles an inverted form of the activity

in SPL that we interpret as reflecting top-down attention. Therefore, we speculate that TPJ responses index disengagement of the putative bottom-up attention network during performance of an effortful task. That is, during memory-guided decision-making under uncertainty (indexed by long RTs), top-down attention processes in SPL are highly engaged, and bottom-up attention processes in TPJ are suppressed. In this context, the current results parallel findings in the attention literature that suggest a deactivation of ventral PPC during demanding visuospatial tasks (Shulman et al. 2003; Todd et al. 2005; Shulman et al. 2007), and formal meta-analysis revealed that the left TPJ region identified in the present study anatomically overlaps with the left parietal component of the ventral, bottom-up attention network proposed by Corbetta and Shulman (2002) (Fig. 6e). Moreover, there was greater recruitment of right than left TPJ in the current study (as is illustrated by both peak and extent values in Table 2), a pattern that is similar to the hemispheric asymmetry previously reported in the bottom-up attention network (Corbetta et al. 2008).

The current findings are inconsistent with overarching, single-function accounts of ventral PPC. For example, Cabeza et al. (2012) recently proposed that ventral PPC activity across many domains, including episodic retrieval and bottom-up attention, is “largely overlapping with some differences around the edges,” such that episodic retrieval effects in ventral PPC could be described as reflecting the engagement of bottom-up attention. The present data, along with our prior meta-analysis (Hutchinson et al. 2010; see also Figure 6d,e), are not compatible with the assertion that episodic retrieval and bottom-up attention effects in ventral PPC are largely overlapping. First, our meta-analysis revealed anatomically distinct bottom-up attention effects predominantly in TPJ and recollection-related retrieval effects in AnG. Second, the present memory-sensitive left AnG and bilateral TPJ regions were functionally defined using opposing contrasts ([Task and Specific Source > Item Only] and [Item Only > Task and Specific Source], respectively). By definition, these regions were non-overlapping, and our statistically independent ROI analyses of the full pattern of retrieval effects in these regions further confirmed dissociation of their functional patterns. Third, the left AnG and left TPJ regions identified in the present memory study overlaps with the corresponding AnG and TPJ regions identified in our memory and attention meta-analysis (Fig. 6d, e). Collectively, it is clear that left AnG and TPJ exhibit distinct patterns of memory retrieval effects in the present study and that these effects anatomically correspond to the ventral PPC regions commonly reported in studies of episodic recollection and bottom-up attention, respectively. The functional distinctions noted here between TPJ and AnG add to a growing literature that indicates that ventral PPC is comprised of multiple subregions that are distinguished by both functional measures and anatomical connectivity measures (Vincent et al. 2006; Nelson et al. 2010; Mars et al. 2011; Sestieri et al. 2011; Yeo et al. 2011). Moreover, the current ventral PPC findings are consistent with evidence suggesting that anterior and posterior PPC are components of distinct and anticorrelated functional networks (Fox et al. 2005).

Conclusions

A dorsal/ventral parcellation of parietal contributions to episodic memory does not account for the diverse set of

functional responses that we have found within left lateral PPC during episodic retrieval. Instead, at least 4 functionally distinct regions are differentially engaged during episodic retrieval, with lateral IPS and AnG indexing graded differences in item memory strength and recollection, respectively, and SPL and TPJ indexing the engagement of top-down and, more speculatively, bottom-up attention, respectively. Moreover, a subset of the left PPC topographic maps of spatial attention defined within individual subjects displays a similar pattern of activity as the memory-defined SPL, further implicating top-down attentional processes in effortful retrieval decisions. These findings therefore provide empirical support for a role of visuospatial attention in episodic retrieval, while also documenting that 2 additional mechanisms (mediated by left lateral IPS and AnG) are differentially engaged during attempts to remember.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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