

Dissociable parietal regions facilitate successful retrieval of recently learned and personally familiar information

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ABSTRACT

In fMRI analyses, the posterior parietal cortex (PPC) is particularly active during the successful retrieval of episodic memory. To delineate the neural correlates of episodic retrieval more succinctly, we compared retrieval of recently learned spatial locations (photographs of buildings) with retrieval of previously familiar locations (photographs of familiar campus buildings). Episodic retrieval of recently learned locations activated a circumscribed region within the ventral PPC (anterior angular gyrus and adjacent regions in the supramarginal gyrus) as well as medial PPC regions (posterior cingulate gyrus and posterior precuneus). Retrieval of familiar locations activated more posterior regions in the ventral PPC (posterior angular gyrus, LOC) and more anterior regions in the medial PPC (anterior precuneus and retrosplenial cortex). These dissociable effects define more precisely PPC regions involved in the retrieval of recent, contextually bound information as opposed to regions involved in other processes, such as visual imagery, scene reconstruction, and self-referential processing.

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1. Introduction

Neurocognitive analyses of episodic memory have generally focused on the medial temporal lobe (MTL) and prefrontal cortex (PFC), as these regions play a crucial role in memory encoding and remembering (Badre & Wagner, 2007; Davachi, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; Race, Keane, & Verfaellie, 2011; Scoville & Milner, 1957; Squire, Stark, & Clark, 2004). Recent advances, however, have implicated another region, the posterior parietal cortex (PPC), as a prominent neural correlate of episodic retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Shimamura, 2011; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). The PPC has been particularly associated with the *successful retrieval effect* in which correctly recognized items (Hits) are compared to correct rejections (CRs). Under a variety of tests and conditions, the PPC is active when recently learned information is retrieved (Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Konishi, Wheeler, Donaldson, & Buckner, 2000). Given the rather recent appreciation of the PPC to episodic memory, the nature of its contribution remains unclear. In particular, the extent to which retrieval-related activity is associated with other PPC functions, such as spatial processing (e.g., mental imagery, perspective taking, spatial attention) and self-referential processing

remains a topic of interest (Burgess, Becker, King, & O'Keefe, 2001; Hassabis, Kumaran & Maguire, 2007; Moulton & Kosslyn, 2009; Sajonz et al., 2010; Silver, Ress, & Heeger, 2005).

Both medial and lateral PPC regions monitor successful retrieval. Within the lateral PPC, activity has been dissociated such that highly confident or recollective responses are localized in the ventral PPC (vPPC), whereas less confident or familiarity responses are localized in the dorsal PPC (dPPC) (Kim & Cabeza, 2009; Spaniol et al., 2009; Wheeler & Buckner, 2003). As a result, recent analyses of the neural correlates of episodic retrieval have focused on the vPPC as this region consistently shows heightened activity during strong, highly confident recollections of recently learned information. Interestingly, vPPC activity can be elicited by implicit retrievals (Elman & Shimamura, 2011) as well as for false recognitions (Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003), suggesting that non-conscious and subjective experiences of retrieval can also drive PPC activity.

In a recent fMRI study, Elman, Klostermann, Marian, Verstaen, and Shimamura (2012) compared the retrieval of familiar, well-learned (semantic) facts with the retrieval of recently learned (episodic) facts. To assess retrieval, subjects were presented a fact question (e.g., *The sport that is associated with Wimbledon is...*) and were asked to rate their feeling of knowing (FOK) for the answer (from *definitely know* to *guess*). For both familiar and recently learned facts, strong FOKs were associated with broad regional activity in the PPC and PFC. Yet episodic facts—those items that were acquired during a single, contextually bound episode (i.e., the study phase)—elicited greater activity in the

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vPPC (angular gyrus). Familiar facts elicited greater activity in the anterior temporal gyrus, a region known to be involved in semantic processing (Simmons & Martin, 2009)

Within the purview of episodic or autobiographical memory, extant findings suggest a distinction between memory for recently learned, laboratory-based information and memory for personally experienced (everyday) events. Whereas lab-based memory is typically assessed using rather mundane stimuli (words or pictures) and standard test methods (recognition, recall), event memory involves rich autobiographical information and are typically assessed with more open-ended test paradigms, such as the Galton cue method, in which word cues are used to elicit autobiographical memories (McDermott, Szpunar, & Christ, 2009). Such cueing paradigms are complicated by the fact that the quantity, quality, and accuracy of retrieved information are often difficult to evaluate (see Cabeza & Jacques, 2007 for review). McDermott et al. (2009) suggested that while these cueing procedures are useful in emphasizing particular aspects of memory, methodological differences between lab-based and event memory tests may complicate interpretations of results.

As a means of distinguishing the neural correlates of retrieving recent episodic, contextually bound information (e.g., lab-based material) with other retrieval-related spatial processes (e.g., imagery, scene reconstruction), we developed a memory paradigm that assessed these aspects of episodic retrieval using the same test procedure. Prior to scanning, subjects were presented photographs of buildings that they had previously never seen. These stimuli represented items acquired during a single episodic event (i.e., the study phase). At test, these recently-studied buildings were shown with photographs of novel buildings and personally familiar buildings (i.e., buildings on the UC Berkeley campus). For each test item, subjects were asked to determine whether they had seen the building before and to rate their confidence (high versus low). Recognition of frequently encountered buildings, though autobiographical in nature, has some commonalities with retrieval of a familiar fact, as recognition does not necessarily depend upon retrieval of a specific prior episode. Kopelman, Wilson, and Baddeley (1989) refer to memories for such multiply exposed autobiographical information as *personal semantics*. These personally familiar locations are likely represented widely as spatial knowledge or as a part of personal semantics (i.e. “my psychology class is held in Tolman Hall”), whereas memory for studied material is tied to a specific episodic event (i.e., the lab-based learning session). In this manner, much like the study of semantic versus episodic facts (Elman et al., 2012), we were able to distinguish neural responses to recently learned items from responses to previously familiar items using the exact same retrieval cues. Yet, unlike the previous study, we assessed retrieval of visuospatial information in the form of recently presented buildings versus personally familiar buildings.

The analysis of visuospatial memory is important as the PPC has been linked to a variety of other spatial processes, such as visual attention, mental imagery, and scene reconstruction (Burgess, Becker, et al., 2001; Byrne, Becker, & Burgess, 2007; Palermo, Ranieri, Nemmi, & Guariglia, 2012; Summerfield, Hassabis, & Maguire, 2010; Vogeley & Fink, 2003). For example, mental imagery from a first-person, egocentric perspective has been associated with PPC activity (Byrne et al., 2007; Vogeley & Fink, 2003) as has the processes underlying mental scene reconstruction (Henderson, Larson, & Zhu, 2008; Summerfield et al., 2010). Additionally the vPPC is also thought to play a role in self-referential processing and is part of a core autobiographical memory network (Sajonz et al., 2010; Svoboda, McKinnon, & Levine, 2006). Given such findings, PPC activity during episodic retrieval may be related more generally to processing self-referential information or spatial details rather than the processes associated with retrieving specific episodic events. If so, then it is

predicted that retrieval of personally familiar locations would be particularly effective in engaging the vPPC, as retrieval of such information would be associated with a rich set of autobiographical, egocentrically based recollections that would depend significantly on mental scene reconstruction.

There are, however, findings and theoretical perspectives that identify the vPPC as specifically related to the retrieval of episodically encapsulated information. According to the *Attention to Memory (AtoM)* model (Cabeza, 2008; Cabeza, Ciaramelli, & Moscovitch, 2012) the vPPC is responsible for bottom-up attentional capture of event features by memory signals output by the MTL. Such processes are particularly active during recollective responses when there is thought to be a large amount of mnemonic details relevant to the particular event being retrieved. Shimamura (2011) proposed that the vPPC is involved in the *cortical binding of relational activity (CoBRA)*, such that this region acts as a convergence zone that links event features associated with specific, contextually bound events. Strong episodic recollections rely particularly on such bindings, because they involve reinstatement of the ensemble of event features that make up a specific episodic memory. Vilberg and Rugg (2008) suggested that vPPC acts as an episodic buffer that stores and collects multimodal event features during retrieval. Although these theories define episodic recollection in different ways, they all predict that the vPPC should be particularly engaged during the retrieval of information from a specific, contextually bound event.

An additional possibility remains that distinct sub-regions within the vPPC underlie these various processes and that the focus of activity within the vPPC may depend on the mnemonic qualities being retrieved. There is evidence to suggest that the PPC may be delineated beyond the dorsal–ventral split described above. It appears that memory-related activation are localized to more posterior vPPC regions (angular gyrus), whereas activation in more anterior regions (such as the supramarginal gyrus) may reflect stimulus-driven visual attention (Cabeza et al., 2012; Hutchinson, Uncapher, & Wagner, 2009; Nelson et al., 2010). While activations are reported with foci falling within in a range of areas (with labels such as the inferior parietal lobule (IPL), angular gyrus, temporo-parietal junction (TPJ) and BA39), it is commonly assumed that these results represent common activity arising from a homogeneous brain region. However, recent evidence drawing on functional and structural connectivity suggests that perhaps a greater level of functional heterogeneity exists within these regions than has previously been assumed (Caspers et al. 2012; Mars et al. 2012; Nelson et al., 2010). In particular the angular gyrus itself may consist of anterior and posterior functional divisions. An open question remains regarding how the characteristics information retrieved during a given task influences the focus of activation within the vPPC.

The present study contrasted memory for information learned during a single episode (i.e., the study phase) with memory for familiar spatial locations. We attempted to reduce methodological differences between the retrieval of these two types of episodic retrieval by testing memory with identical retrieval cues, test method, and response decisions. In this manner, we could determine the degree to which vPPC activity is related specifically to retrieving information bound by a single episodic event or whether it more generally monitors other aspects of spatial retrieval, such as mental imagery, egocentric perspective taking, or scene reconstruction.

2. Methods

2.1. Participants

Nineteen healthy subjects were included in this study (mean age 21.63 years, range 19–29 years; 10 females). Four additional subjects were excluded from analysis due to excessive head motion and scanner artifact, and a further four

subjects were excluded due to poor behavioral performance (these subjects all had less than 33% hit rate or correct rejection rate). Recruitment was conducted via advertisement on the Department of Psychology website (<http://psychology.berkeley.edu/rsvp>), with the criterion that they had been enrolled at UC Berkeley for at least two years and were familiar with the campus. All subjects were native English speakers and were right-handed. None of the subjects reported a history of neuropsychiatric disorders or brain injury or having recently taken psychoactive medication. Subjects were paid for their participation and gave informed consent according to guidelines approved by the UC Berkeley Office for the Protection of Human Subjects.

2.2. Stimuli

Ninety photographs of buildings were used in this study. Of these, 30 consisted of buildings from the UC Berkeley campus considered to be very familiar amongst students were used for the “Personally Familiar” locations. The remaining 60 photographs consisted of unfamiliar buildings taken at the CSU East Bay and Mills College campuses and downloaded from the web. Both the familiarity of the UC Berkeley buildings and the unfamiliarity of the other set of buildings (subjects had not visited the other campuses) were verified by a follow-up questionnaire at the end of the experiment. Half of the unfamiliar buildings were presented during a study phase and comprised the “Studied” items, while the other buildings were presented only at test and used as “New” items in a recognition test. Buildings used in the “Studied” and “New” sets were counter-balanced across subjects.

2.3. Behavioral procedure

All trials were presented using *E-Prime 2 Professional* software (<http://www.pstnet.com/eprime.cfm>). Prior to scanning, participants were presented a study phase in which the 30 study buildings were presented two times each in a pseudo-random order. On each trial, participants were shown a building and given 4000 ms to determine whether it was the first or second presentation. Trials were separated by a 1000 ms blank screen (see Fig. 1).

In the scanner, approximately 30 min after the study phase, participants were given a recognition test. A total of 90 test items (30 Studied, 30 Personal, 30 New) were presented in two scanning blocks (see Fig. 1). Each trial consisted of a photograph of a building for 3500 ms followed by a central fixation cross presented for a jittered ITI (900–5300 ms, mean=1975.5 ms). Participants were asked to rate each item with respect to whether or not they have seen it before, either during the experiment or in their day to day lives. No distinction as to when or where they previously encountered the building was necessary; the mnemonic decision remained the same for each condition. The response options were: “Definitely seen the building before” (referred to as high confidence (HC) hits), “Maybe seen the building before” (referred to as low confidence (LC) hits), or

“Definitely not seen the building before” (referred to as “new”). These response options map onto those associated with the Remember/Know paradigm, though they are less theoretically motivated. That is, they do not necessarily imply a discrete, dual-process interpretation (Shimamura, 2010), but rather a subjective measure of response confidence. Responses were made using key-presses on a response box with finger-key-press mappings counterbalanced across subjects.

After scanning, we administered a questionnaire regarding how long participants had been enrolled at UC Berkeley and whether they had previously visited the CSU East Bay campus or Mills College. No participants reported having visited these other campuses.

2.4. fMRI acquisition

Subjects were scanned with a 3T Siemens (Erlangen, Germany) Trio scanner housed at the UC Berkeley Brain Imaging Center. For each of the two functional runs, we used a T2*-weighted echo-planar imaging (EPI) sequence [TR=2200 ms; TE=26 ms; flip angle=80°; matrix=100 × 100; FOV=210 mm; 3 mm slice thickness] with GRAPPA [acceleration factor 2]. Thirty-five axial slices oriented to the AC-PC were acquired in a sequential descending order giving whole brain coverage. A total of 130 volumes were collected during each of the functional imaging runs. The first nine volumes of each run were discarded to allow for magnetization preparation. A high resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) [TR=2300 ms; TE=2.98; matrix=256 × 256; FOV=256; sagittal plane; slice thickness=1 mm; 160 slices] and a gradient-echo multislice (GEMS) [TR=250 ms; TE=22; matrix=256 × 256; FOV=256; 3 mm slice thickness, 37 slices] were collected for registration purposes.

2.5. fMRI data analysis

Data were preprocessed and analyzed with the FSL toolbox v4.1.7 (<http://www.fmrib.ox.ac.uk/fsl>; (Smith et al., 2004). Motion correction was performed with MCFLIRT, aligning all images to the middle slice with rigid body transformation. Slice timing correction was performed using (Hanning windowed) sinc interpolation to shift each slice in the volume in reference to the middle of the TR period. BET (brain extraction tool) was then used to create a mask of the brain from the first volume of each time series and used to separate brain from surrounding skull and tissue in each volume. All images were spatially smoothed with a 5 mm FWHM Gaussian kernel to reduce noise and allow group analysis. High-pass temporal filtering was performed using the local Gaussian-weighted fit of a running line to remove low frequency artifacts. Subject data was registered to standard space in a two-step process using FLIRT (FMRIB’s Linear Image Registration Tool). First, EPIs were registered to each subject’s skull-stripped high resolution T1-weighted image. Second, subject’s T1-weighted images were registered to standard (MNI) space (FSL’s MNI152 template). The two registrations

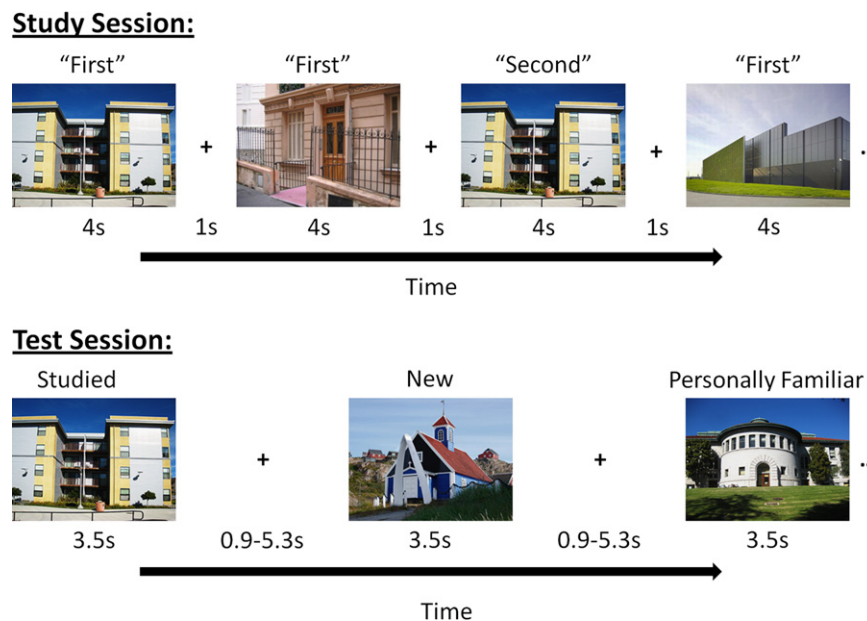


Fig. 1. The study session presented 30 photographs of previously unfamiliar buildings, each shown twice in a pseudo-random order. Subjects responded whether it was the first or second presentation for each. The test session took place approximately 30 min later in the fMRI scanner. Subjects were presented 30 Studied buildings, 30 Personally Familiar (from the UC Berkeley campus), and 30 New buildings over two blocks. For each photograph, subjects were asked to respond whether they had “Definitely seen the building before,” “Maybe seen the building before” or “Never seen the building before.”

were then combined to take the subject's EPI images and run-level statistical maps into standard space.

A multi-level, mixed effects general linear model was run using FILM (FMRIB's Improved Linear Model) which treated subjects as random effects. Individual runs from the test phase were modeled in subject space and resulting statistical maps were registered to standard space for higher level analysis. Regressors of interest were obtained by convolving stimulus onset times with FSL's double-gamma hemodynamic response function and the temporal derivative. Each correct response type was modeled separately for both "Studied" and "Personal" conditions of both confidence levels (HC or LC) and for correctly identified "new" items. Incorrect responses and trials with no response were modeled as regressors of no interest. Motion parameters were included as additional confound variables and temporal autocorrelation was removed through pre-whitening. Contrasts were entered comparing both Studied and Personal items to new items as well as direct comparisons of Studied and Personal items to each other.

A second level analysis combined the runs for each subject using a one-sample *t*-test, treating runs as fixed effects. Third-level group statistical maps were created for each contrast using FLAME (FMRIB's Local Analysis of Mixed Effects). FLAME implements a Bayesian two-stage model, the first being a fast approach to the posterior probabilities of activation for each voxel and the second uses a slower Markov Chain Monte Carlo (MCMC) based analysis for all voxels identified as being near threshold in the first stage. The whole brain family-wise error was corrected to $P < 0.05$ using Gaussian Random Field theory with a cluster forming threshold of $z > 2.3$.

3. Results

3.1. Behavioral results

Recognition performance was numerically higher for Personal (90.5% correct) compared to Studied items (85.6% correct), although the difference was not significant, [$t(18) = -1.551$, $p = 0.13$] (see Table 1). A significantly higher proportion of HC ratings were given to Personal items (81.1%) than to Studied items (71.8%), [$t(18) = 2.06$, $p < 0.05$]. However, the proportion of HC responses was relatively high in each condition, indicating a strong feeling of subjective confidence on the majority of trials. Response latencies were also comparable between the two sets (Studied = 1532 ms; Personal = 1469 ms, [$t(18) = 1.095$, $p = 0.28$]). However, response latencies for New items (1800 ms) were significantly slower than latencies for the Studied and Personal sets ($t(18) > 5.2$, $p < 0.001$).

3.2. fMRI results

Retrieval-related activations (Hits-CRs) were assessed separately for Studied and Personal items (see Fig. 2). Within the vPPC, Studied items activated a large cluster centered on the anterior angular gyrus and extending into adjacent regions in the supramarginal gyrus and intraparietal sulcus (IPS). In the PFC, active regions included the left dorsolateral prefrontal cortex (dlPFC), frontal pole, and medial prefrontal cortex (mPFC). Significant activations also occurred in medial regions, including the anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), and precuneus (see Table 2 for full set of activations).

For Personal items, retrieval-related activations within the vPPC occurred in more posterior regions than those observed

for Studied items. Specifically, Personal items activated the posterior angular gyrus and adjacent regions in the lateral occipital complex (LOC). Within the angular gyrus, mid-regions were activated by both Personal and Studied items (see Fig. 2). Within the PFC, Personal items activated left dlPFC (inferior frontal gyrus) and polar regions. Particularly extensive regions of activation were observed in medial regions, including ventromedial PFC, anterior precuneus and adjacent regions in the retrosplenial cortex (see Table 2).

To assess retrieval-related activations specific to Studied and Personal items, we performed bidirectional contrasts between these two conditions for HC hits (see Fig. 3). We interpreted these HC contrasts to define regions associated with very strong memorial responses that are often localized to ventral parietal areas. As was shown for overall hits > CRs, HC hits for Studied items relative to Personal items activated bilateral regions in the anterior angular gyrus and adjacent regions in the supramarginal gyrus and IPS, whereas the reverse contrast (HC Personal items > HC Studied items) activated posterior angular gyrus and LOC. Dissociable activations were also observed in medial regions, as HC Studied items specifically activated right dlPFC, anterior PFC (aPFC), and posterior cingulate, whereas HC Personal items activated primarily left superior and bilateral medial frontal cortex as well as bilateral activations in the anterior precuneus, retrosplenial cortex, medial PFC, and parahippocampal gyrus (for full set of activation sites, see Table 3). We additionally compared Studied and Personal items collapsed across confidence levels to assess more broadly retrieval-related activity. This contrast resulted in similar areas of activity with the addition of clusters in the dPPC and posterior precuneus for the Studied > Personal contrast (see Supplementary Fig. S1 and Table S1 for full set of activations).

4. Discussion

Recognition memory was assessed for spatial locations (photographs of unfamiliar buildings) presented during a single study phase and for personally familiar spatial locations (photographs of familiar campus buildings). For each test item, participants determined whether they had previously seen the item and rated their confidence. The successful retrieval of both recently learned and familiar buildings engaged a broad cortical network that included regions in the lateral PPC, medial PPC, MTL, and PFC. These regions generally conform to the *default mode network* (DMN) as well as regions commonly observed during episodic and autobiographical retrieval, scene construction, spatial navigation and self-referential processing (Burgess, Maguire, Spiers, & O'Keefe, 2001; Konishi et al., 2000; Maguire, 2001; Northoff et al., 2006; Spreng, Mar, & Kim, 2009). Within these regions, however, distinctly dissociable activations were observed.

4.1. Lateral PPC

With respect to the successful retrieval effect (Hits > CRs), Studied items activated a vPPC region centered in the anterior angular gyrus which extended into the supramarginal gyrus and IPS. This region was distinct from activations associated with successful retrieval of Personal items, which involved posterior angular gyrus and adjacent regions in the LOC. The dissociation of vPPC activity for Studied and Personal items was particularly apparent when HC hits were contrasted between conditions (see Fig. 3). Previous findings have implicated the vPPC during recollection-based episodic retrieval (Cabeza, 2008; Shimamura, 2011; Vilberg & Rugg, 2008), and the present findings point to a more focal region centered on the anterior angular gyrus as particularly involved in the retrieval of information from a

Table 1

Behavioral results from the test phase of the experiment. Proportion of response types for each condition is listed. The "Old" column refers to the combined percent of "High" and "Low" confidence responses. Recognition performance was similar for Studied and Personal items. However, subjects were significantly more likely to give high confidence responses for Personal items than Studied items.

	High confidence old	Low confidence old	Old	New
Studied	71.2%	14.4%	85.6%	14.4%
Personal	81.1%	9.4%	90.5%	9.5%
New	8.4%	25.1%	33.5%	66.5%

Table 2

Successful retrieval effect as indicated by peak activations of significant clusters from the contrasts for Studied Items (Hits > CRs) and Personal Items (Hits > CRs). Region labels were derived from the Harvard–Oxford Cortical Atlas.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
<i>Studied Items (Hits > CRs)</i>					
Angular gyrus	L	-54	-56	30	4.14
	L	-38	-54	34	3.53
	L	-52	-54	52	3.38
	R	44	-50	48	3.45
Anterior cingulate	R	10	40	16	3.74
Frontal orbital cortex	L	-24	22	-24	3.91
	L	-32	16	-22	3.52
	L	-14	34	-22	3.25
	L	-18	32	-24	3.13
Frontal pole	L	-28	20	-12	2.78
	L	0	58	20	3.77
	L	-28	46	-18	3.66
	L	-40	44	-10	3.56
	L	-42	56	4	3.24
	L	-42	54	8	3.19
Inferior temporal gyrus	L	-40	50	2	3.16
	L	-48	38	16	3.16
	R	56	-36	-14	3.31
	L	-30	8	-16	3.27
Insular cortex	L	-42	-60	44	3.69
Lateral occipital cortex	L	-42	-70	34	3.48
	R	40	-66	46	3.54
Middle temporal gyrus	L	-66	-36	-18	3.89
	L	-60	-34	-8	3.78
	L	-60	-30	-8	3.6
	L	-66	-32	-14	3.45
	L	-56	-34	-6	3.37
	L	-66	-28	-10	3.18
	R	60	-44	-2	3.82
	R	64	-26	-16	3.46
	R	72	-28	-16	3.44
	R	66	-42	-6	3.34
	R	72	-24	-12	3.24
	Paracingulate gyrus	L	-2	48	10
L		-6	34	26	3.45
R		2	44	18	3.66
R		6	50	-2	3.55
Posterior cingulate	L	-4	-30	44	3.68
	L	-2	-40	40	3.65
	L	0	-28	44	3.61
	L	0	-50	32	3.53
	R	4	-26	44	3.64
Precuneous cortex	L	-8	-72	28	3.73
Supramarginal gyrus	L	-56	-50	24	3.5
	R	42	-44	34	3.55
	R	46	-42	48	3.54
	R	54	-36	48	3.52
	R	56	-38	42	3.31
<i>Personal items (Hits > CRs)</i>					
Frontal medial cortex	L	-6	54	-16	4.76
	L	-8	38	-16	4.75
	L	-50	28	-12	3.48
Frontal pole	L	-4	58	6	5.27
	L	-4	58	0	4.98
	L	-2	56	-12	4.78
	L	-52	38	-2	3.76
Inferior frontal gyrus	L	-52	28	14	3.91
	L	-52	34	10	3.66
	L	-52	30	8	3.6
	L	-44	22	22	3.39
Lateral occipital cortex	L	-50	-72	30	5.11
	L	-38	-76	32	4.65
	L	-46	-80	30	4.47
	L	-54	-72	32	4.16
	L	-32	-86	32	4.12
	L	-38	-84	36	3.94
	R	52	-64	18	3.91
	R	50	-64	22	3.87
	R	56	-64	18	3.87
	R	40	-78	42	3.55
	R	44	-72	28	3.29
	R	40	-78	34	3.08

Table 2 (continued)

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Middle temporal gyrus	L	−62	−8	−20	4.42
	L	−54	0	−26	4.35
	L	−52	−8	−24	3.92
	L	−56	−8	−14	3.52
Paracingulate gyrus	L	−8	32	−12	4.84
	L	−6	−56	28	5.39
Posterior cingulate	L	−2	−54	20	4.92
	L	−2	−64	34	5.22
	L	−4	−54	12	4.86
	L	−14	−58	18	4.68
Precuneous cortex	L	−4	−62	42	4.67
	L	−54	4	−30	3.37
	L	−50	18	−34	3.1

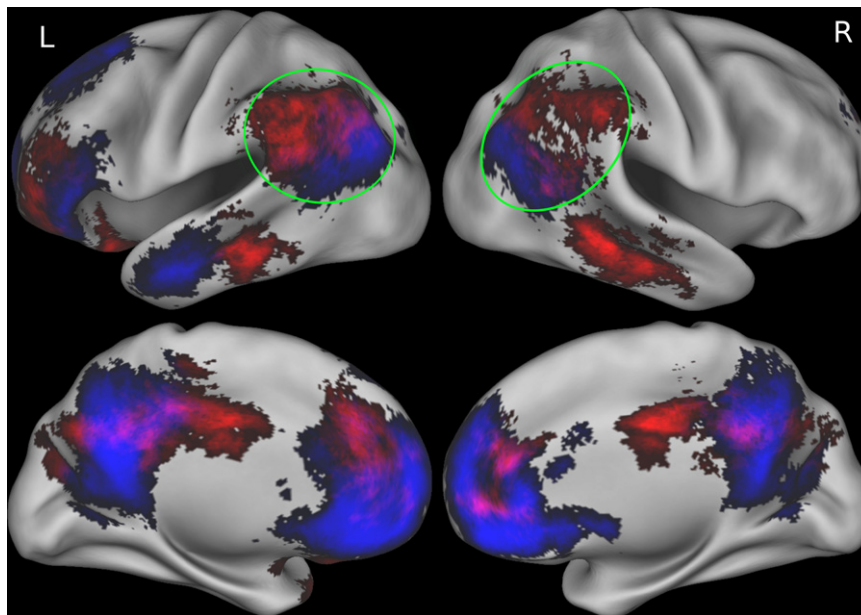


Fig. 2. The successful retrieval effect (Hits > CRs) for Studied (red) and Personal (blue) Items with areas of overlap shown in purple. Within the vPPC (circled), Studied items activated anterior regions, whereas Personal items activated more posterior regions (with overlapping areas in mid-regions of the angular gyrus). Note extensive retrieval-related activations for Personal items in medial regions. All clusters were significant after correction for multiple comparisons. Activations are projected on to lateral (top) and medial (bottom) views of an inflated atlas using CARET software (Van Essen, 2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

specific episodic context (Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wheeler & Buckner, 2004). A recent study by (Hirshhorn, Grady, Shayna Rosenbaum, Winocur, & Moscovitch, 2012) also found greater activity in the angular gyrus when subjects made judgments based on memory for a specific experience within an environment compared to spatial judgments about relative locations of environments.

Retrieval of familiar locations activated a more posterior vPPC region, which was centered in the posterior angular gyrus and extended into the LOC. This regional activation can be related to extant findings, such as those by Nelson et al. (2010) in which a functional connectivity analysis of task-based and resting-state fMRI was used to parcellate the left PPC into functionally distinct sub-regions. They found functional networks linked to the anterior and posterior inferior parietal lobule adjacent to the IPS that were dissociable from another network tied to more inferior and posterior angular gyrus and extending into LOC. In a meta-analysis of retrieval tasks, McDermott et al. (2009) found that activity for recently studied, lab-based material was localized in anterior regions of the angular gyrus, whereas retrieval of

autobiographical information was localized more posteriorly into the LOC. Hassabis et al. (2007) argued that posterior vPPC regions may be more accurately described as engaging in scene construction. This proposal is based upon findings that the posterior angular gyrus is active when subjects imagine scenes compared to simple objects.

Our results are also consistent with findings of a functional dissociation in which successful episodic retrieval was associated with activity in anterior and superior vPPC regions, whereas self-referential processing was associated with activity in inferior and posterior regions (Sajonz et al., 2010). Finally, the left parietal cluster in the posterior angular gyrus observed in the present study for familiar items overlapped with a region active when subjects were asked to make judgments based on spatial information rather than episodic details (Hirshhorn et al., 2012).

4.2. Medial PPC

Retrieval of Studied and Personal items also activated broad regions in the medial PPC in both hemispheres. As with lateral

Table 3

Peak activations of significant clusters from the contrasts of High confidence Studied vs. High confidence Personal responses. Region labels were derived from the Harvard-Oxford Cortical Atlas.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
<i>High confidence studied > High confidence personal</i>					
Angular gyrus	L	-40	-58	48	5.14
	L	-42	-48	36	3.34
	R	44	-50	46	5.17
Central opercular cortex	L	-48	-12	18	3.64
	R	58	-14	20	3.21
	R	68	-12	10	3.17
	R	60	-12	12	3.11
Frontal orbital cortex	R	46	20	-6	3.16
Frontal pole	L	-36	50	0	3.62
	L	-40	56	6	3.42
	L	-34	58	-4	3.33
	L	-38	60	10	3.24
Frontal pole	R	44	54	4	3.97
	R	42	58	8	3.71
	R	36	40	10	3.59
	R	38	56	-2	3.48
	R	38	46	12	3.25
	R	40	44	4	3.2
Heschl's gyrus	L	-50	-26	10	3.21
Insular cortex	R	28	16	8	3.65
	R	44	16	-10	3.4
	R	42	-2	-10	3.08
Lateral occipital cortex	L	-40	-66	52	3.66
Middle frontal gyrus	L	-40	38	30	3.7
	L	-42	30	28	3.4
Parietal operculum cortex	R	58	-22	16	3.79
	R	52	-20	22	3.6
Planum polare	R	54	2	-2	3.6
Planum temporale	L	-58	-24	12	3.41
Posterior cingulate	L	-2	-36	24	3.44
	R	4	-20	26	4
	R	8	-26	26	3.99
	R	6	-40	22	2.57
	R	10	-36	22	2.49
Superior parietal lobule	L	-36	-54	52	4.33
	L	-32	-58	56	3.77
	L	-42	-48	50	3.63
	R	38	-44	54	3.71
	R	34	-52	54	3.12
Supramarginal gyrus	L	-64	-32	26	4
	L	-60	-26	26	3.85
	L	-62	-28	20	3.81
	R	54	-22	26	3.86
	R	48	-28	44	3.29
	R	48	-38	48	3.26
	R	52	-34	56	3.16
Temporal pole	R	46	12	-10	3.23
<i>High confidence personal > High confidence studied</i>					
Angular gyrus	L	-44	-62	16	2.85
Frontal medial cortex	L	-6	54	-10	5.83
	L	-8	46	-12	5.42
	L	-4	34	-16	5.38
	L	-2	50	-14	5.08
	R	4	48	-10	5.18
Frontal pole	L	-18	40	44	4.18
	L	-18	44	42	3.98
Hippocampus	L	-24	-16	-20	3.56
	R	32	-20	-16	3.71
Lateral occipital cortex	L	-36	-82	30	5.38
	L	-50	-72	22	4.93
	L	-46	-78	24	4.49
	L	-40	-70	20	4.23
	L	-50	-76	34	3.63
	R	42	-82	28	4.34
	R	36	-82	32	4.25
	R	48	-68	22	3.89
	R	32	-88	32	3.66
	R	44	-62	22	3.54
	R	48	-74	24	3.5
Lingual gyrus	L	-8	-58	4	5.7
	L	-12	-62	4	5.35
Middle frontal gyrus	L	-26	36	44	3.3

Table 3 (continued)

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Paracingulate gyrus	L	0	46	–10	5.46
Parahippocampal gyrus	L	–20	–38	–18	4.57
	R	26	–38	–14	3.73
Precuneous cortex	L	–6	–62	12	5.44
	L	–12	–60	14	5.31
	L	10	–52	4	5.17
	R	14	–58	16	6.1
Superior frontal gyrus	L	–22	22	44	4.01
	L	–16	38	34	3.38
	L	–22	22	34	2.94

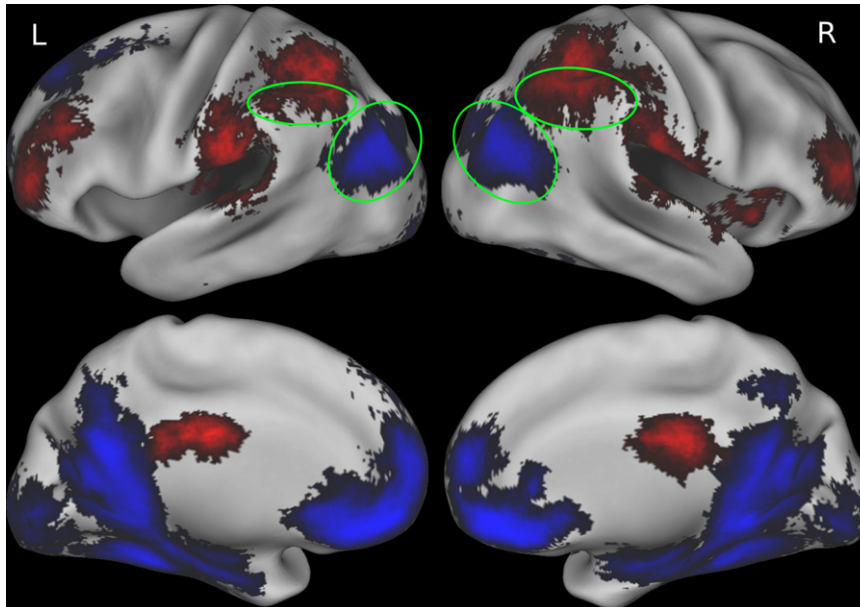


Fig. 3. Clusters in which there was greater activity for Studied compared to Personal items (red) and Personal compared to Studied items (blue). Only high confidence responses were included in this contrast in order to match response confidence between the conditions. Of particular interest are the anterior–posterior dissociations within lateral vPPC (circled) and medial parietal cortices. All clusters were significant after correction for multiple comparisons. Activations are projected on to lateral (top) and medial (bottom) views of an inflated atlas using CARET software (Van Essen, 2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

PPC activations, medial activations were dissociable between the two types of stimuli. Whereas Studied items activated posterior cingulate gyrus and posterior precuneus, Personal items activated more anterior medial PPC regions, such as the anterior precuneus and retrosplenial cortex (see Fig. 3 and Supplementary Fig. S1). Interestingly, the precuneus has been associated with scene construction (Hassabis et al., 2007) as well as first-person perspective taking (Vogeley & Fink, 2003). In contrast, the posterior cingulate gyrus was found to be engaged during episodic retrieval over and above activity associated with scene construction (Hassabis et al., 2007). Thus, as with the anterior–posterior dissociation observed in the lateral PPC for Studied and Personal items, there was a comparable posterior–anterior dissociation observed in the medial PPC.

Findings related to the functional properties of precuneus activity are consistent with the dissociations observed in the present study (Cavanna & Trimble, 2006). In particular, activation of the posterior precuneus and posterior cingulate gyrus has been related to successful retrieval effects, whereas anterior precuneus and retrosplenial cortex activations has been related to self-referential or visuospatial processing engaged by mental imagery from a first-person perspective (Cabeza et al., 2004; Maguire, 2001; Sajonz et al., 2010; Summerfield, Hassabis, & Maguire, 2009; Svoboda et al., 2006). It is also worth noting that the

precuneus is more active for recent memories (Nadel, Campbell, & Ryan, 2007; Söderlund, Moscovitch, Kumar, Mandic, & Levine, 2012). The relationship between precuneus activity and recency is often attributed to the greater level of imagery and vividness associated with these memories. Our results support this explanation as we found greater activation for Personal items which involved retrieval of remote yet potentially richly detailed autobiographical memories.

4.3. MTL and PFC

Significant bilateral activity was observed in the parahippocampal gyrus for Personal items but not for Studied items. Such activations may reflect the contribution of this region to spatial processing, such as scene reconstruction and spatial integration (Cabeza & Jacques, 2007; Gilboa, 2004; Henderson et al., 2008; Summerfield et al., 2010; Vann, Aggleton, & Maguire, 2009). The parahippocampal gyrus has also been functionally associated with activity in the vPPC and retrosplenial cortex, suggesting a posterior circuit involved in egocentric spatial processing (Burgess, Becker, et al., 2001; Burgess, Maguire, et al., 2001; Maguire et al., 1998). It is likely that recognition of personally familiar buildings activated this posterior cortical circuit as such information is represented by egocentric spatial knowledge

of buildings and their surroundings. The influence of recency on our results remains unclear. It has been argued that hippocampal activity varies with memory type rather than memory recency, and alternatively, that hippocampal activity varies non-linearly over time (Maguire, Henson, Mummery, & Frith, 2001; Söderlund et al., 2012). We are precluded from assessing this question directly as the relative recency of our stimuli was not controlled.

With respect to PFC processes, the right aPFC and dlPFC were more active for Studied items compared to Personal items, whereas the mPFC and vmPFC were more active for the reverse contrast (see Fig. 3). These findings are broadly consistent with meta-analyses of lab-based vs. autobiographical memory (Gilboa, 2004; McDermott et al., 2009; Svoboda et al., 2006). Our present results along with these extant findings, point to mPFC activations as reflecting executive processes related to self-referential analyses. Moscovitch and Winocur (2002) (see also Gilboa, 2004) proposed that mPFC regions underlie “felt rightness” or the ability to gauge quickly the accuracy of a response without the need for in-depth monitoring or verification which may arise from subjects’ strong familiarity. This proposal, however, is in contrast to aPFC and dlPFC activations observed during the successful retrieval of Studied items which may require more monitoring and verification that retrieved items do indeed belong to a specific episodic context (Gilboa, 2004; Svoboda et al., 2006).

4.4. Theoretical implications

The functional dissociations in retrieval-related activity between recently learned and personally familiar information advance our understanding of the neural correlates of episodic retrieval. Whereas anterior vPPC and posterior mPPC regions were engaged during the successful retrieval of recently learned, contextually bound information, posterior vPPC and anterior mPPC regions were engaged during the successful retrieval of personally familiar items. With respect to lateral vPPC regions, previous findings have not distinguished processes associated with explicit episodic retrieval from spatial processes that might contribute to retrieval, such as visual imagery and scene reconstruction. The present findings now point to the anterior angular gyrus as being the focal point for activations associated with retrieval of episodic, contextually bound, information. Furthermore, these results lend support to recent suggestions that the vPPC is composed of functionally dissociable sub-regions (Hutchinson et al., 2012; Nelson et al., 2010). An appreciation of the functional heterogeneity within this area may inform theoretical models and serve to resolve seemingly conflicting patterns of activity within the PPC (Cabeza et al., 2012; Hutchinson et al., 2009).

These findings can be related to theoretical models of episodic memory. AtOM predicts that vPPC should be particularly engaged by the bottom-up capture or reinstatement of event features (Cabeza et al. 2012). By this view, it must be assumed that retrieval of Studied items involved more bottom-up attentional processes than Personal items, perhaps because the pictures used at test for Studied items were perceptually identical to the study material itself and therefore provide a highly relevant retrieval cue. CoBRA (Shimamura, 2011) suggests that the vPPC acts as a convergence zone that binds event features related to specific episodic events. As all Studied items were learned within a single episode (i.e., the study phase), high confident recognition responses should depend specifically on linking items to this specific episode. With respect to the episodic buffer, the vPPC acts to integrate multimodal features within working memory during retrieval. It is thus possible that the retrieval of a specific context requires a greater degree of multi-modal integration compared to personally familiar items. While this experiment was not meant to test between these theories, the results provide strong evidence that

distinguishes retrieval-related activity arising from contextually bound memories in the anterior angular gyrus from activity associated with other processes, such as visual imagery, scene reconstruction and self-referential processes in the posterior angular gyrus.

Although significant differences were observed between Studied and Personal items, two caveats should be mentioned. First, as mentioned above, Studied items were cued during the recognition test with the identical stimuli, namely photographs of buildings that were presented during study. Personal items were cued with photographs of familiar buildings, but the photographs themselves were not previously presented. It is possible that differential activity reflected the monitoring of a perceptual match between study items and test cues, and thus our findings, such as greater activity in the anterior angular gyrus, might have been driven by greater item-cue similarity for Studied items. Yet vPPC activity has been found to correlate with the subjective experience that an item was been previously encountered, even for false recognition of new items in which cue-target overlap is non-existent (Wheeler & Buckner, 2003). Moreover, the greater overlap between recognition cues and the studied material may further emphasize the association of retrieved information with a specific context (i.e. the study session).

Additionally, the test method used in this experiment was meant to contrast retrieval of items presented within a single episodic context and retrieval of items experienced on many occasions. Care was taken to control for task demands during the recognition test, such that memory performance was driven by comparable test cues (photographs of buildings) and responses (old/new recognition with confidence ratings). Despite the novel method of assessing lab-based and event-based memories while controlling for task demands, the quality of the representations accessed by the test must be inferred indirectly. Studied items were presented once and recently within a single learning episode, whereas Personal items were likely experienced on multiple occasions and linked to rather rich autobiographical associations. Our point is that Studied items had to be accessed by referencing a specific episodic event, whereas Personal items were represented more broadly as the event boundaries during which these locations are experienced become blurred with repeated exposures. The findings of doubly dissociable activations between Studied and Personal items suggest that retrieval was driven by qualitatively different processes. To assess more directly underlying features of episodic memory (e.g., lab-based versus event-based), further analyses using even more precise control of to-be-remembered information are required.

In summary, the present study identified dissociable activity between the retrieval of recently presented visuospatial information and previously familiar spatial locations. In the vPPC, retrieval of recently learned information activated the anterior angular gyrus, whereas retrieval of previously familiar locations activated posterior angular gyrus and LOC. In the medial PPC, recently learned items activated the precuneus and posterior cingulate gyrus, whereas familiar items activated the retrosplenial cortex and more anterior regions in the posterior cingulate gyrus. These dissociable effects help to define more precisely neocortical regions involved in the retrieval of recent, contextually bound information as opposed to regions involved in processing other aspects of memory, such as visual imagery, egocentric perspective taking, and self-referential processing.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2012.12.013>.

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