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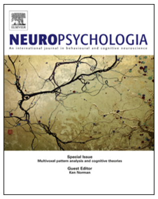

The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity

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ABSTRACT

Numerous neuroimaging studies have shown a dissociation within the left posterior parietal cortex (PPC) between recollection and familiarity, with dorsal regions routinely active during familiarity and ventral regions active during recollection. The two most common methods for separating the neural correlates of these retrieval states are the remember/know paradigm and tests probing source memory. While relatively converging results have been found using these methods, the literature is lacking an adequate and direct comparison of the two procedures. We directly compared these two methodologies and found differences in both the magnitude and extent of activation within the left PPC. During familiarity, dorsal PPC regions were more strongly activated by the source test, while the remember/know test led to stronger recollection-related activations within the ventral regions of the PPC. This modulation of PPC activity is particularly important because it suggests that the neural correlates of familiarity and recollection depend on how they are operationalized. Previous assumptions that remember/know and source memory tests are functionally equivalent should therefore be re-evaluated. Additionally, any theories attempting to explain the functional role of the PPC during memory retrieval must take these differences into account.

1. Introduction

Both recollection and familiarity can be used to guide memory decisions during a standard recognition memory test (Mandler, 1980). Recollected memories are described as containing information about the study episode, are often contextually rich and vivid, and can involve mentally traveling back in time to the original encoding event (Tulving, 1983). Familiarity on the other hand, refers to memories that are lacking information about the study episode, are without contextual detail, and are often based on an undifferentiated, strength-like memory signal (Mandler, 1980). To isolate the neural regions uniquely associated with recollection and familiarity, one must be able to differentiate which items were retrieved via recollection and which relied on familiarity. By far, the two most common strategies for operationalizing recollection and familiarity during neuroimaging studies are the remember/know test and tests probing source memory. During a remember/know test, the subject is asked to identify what retrieval state (recollection or familiarity) was experienced on a trial-to-trial basis (Tulving, 1985). Source tests take a much more objective approach, operationalizing the retrieval state according to whether or not recognition was accompanied by the recovery of a specific piece of contextual information (Johnson, Hashtroudi, & Lindsay, 1993). Both methods have been criticized in the literature, the remember/know test for its subjective nature and exclusive reliance on the subject's ability to correctly classify their retrieval state (Rotello, Macmillan, Reeder, & Wong, 2005; Donaldson, 1996; Dunn, 2004, 2008; Wixted, 2007; Wais, Mickes, & Wixted, 2008), and the source test for being too restrictive on what qualifies as a recollected response (i.e. the 'non-criterial problem') (Yonelinas & Jacoby, 1996). Despite these differences in procedural methodology, there seems to be a general assumption that these methods are essentially functionally equivalent, and as a result are often used interchangeably to separate familiarity and recollection. This ostensible equivalence has been described both at the behavioral level (Yonelinas & Jacoby, 1995) and at the neural level using evidence from event-related potentials (ERP) (Rugg, Schloerscheidt, & Mark, 1998; Mark & Rugg, 1998). In regards to the parietal lobe, both methods have found recollection to be associated with the so called 'parietal old/new effect' which is a positive going deflection that occurs around the 400–800 ms time window (Vilberg & Rugg, 2006; Curran, 2004; Wilding, 2000). Results from functional magnetic resonance imaging (fMRI) studies have also shown a general convergence between these two approaches as to

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what brain regions within the left posterior parietal cortex (PPC) are sensitive to recollection and familiarity. Specifically, both methods have shown a dorsal/ventral dissociation within this area, with familiarity activating more dorsal regions centered around the intraparietal sulcus (IPS) and extending dorsally into the superior parietal lobule (SPL), and recollection activating more ventral regions within the inferior parietal lobule (IPL) (for reviews see: Ciaramelli, Grady, & Moscovitch, 2008; Hutchinson, Uncapher, & Wagner, 2009; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). This apparent convergence is informative because it suggests that the neural representations of familiarity and recollection are the same regardless of the methodology used to index them. While this convergence is somewhat reassuring, the fMRI literature is lacking a direct and adequate comparison of the neural correlates of recollection and familiarity between these two methods. Without this, there remains a possibility that this apparent convergence is merely an illusory finding. If results of such a comparison concluded that different PPC regions were active depending on the test used, this would suggest that these two methods are not as equivalent at measuring recollection and familiarity as is currently assumed. In particular, it would suggest that these divergent brain regions may be representing either a difference in retrieved memory content or a difference in the cognitive demands associated with retrieval depending on what method was used to operationalize recollection and familiarity. Specifically, it could be the case that recollected memories from the source task may be more constrained than memories retrieved via the remember/know task. Additionally, it may be relatively effortful to search for the specific contextual information required by the source test. This increased search effort may engage the top-down attentional system to a greater degree than during the remember/know test. Regardless of what theory is used to explain any differences that might be found, this result would be informative to the field since the standard view is to treat remember/know and source memory tests as equivalent measures of recollection and familiarity. While some fMRI comparisons have been made between the two methods, the vast majority have been conducted between experiments (Ciaramelli et al., 2008; Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). Thus, comparisons have been made across a wide range of stimuli, variations in experimental design, differences in analysis technique, and perhaps most detrimentally, between different subjects. Without controlling for these confounding variables, neural differences between remember/know and source memory tests may be difficult, if not impossible to detect. In other words, even if specific sub-regions of the parietal cortex were more sensitive to one test than the other, co-varying differences in experimental designs may attenuate or even completely mask this effect. Take for instance, the type of stimulus used during testing. Variations in the specific location of neural activity have been found within the left ventral PPC depending on the stimulus type that was used to invoke the activity (Elman, Cohn-Sheehy, & Shimamura, 2013; Klosterman, Loui, & Shimamura, 2009). Research investigating individual differences during recognition memory tests has shown extensive yet reliable differences in brain activity patterns between individuals (Miller et al., 2002, 2009). If variables such as these are free to vary during comparisons of the remember/know and source memory tests, one could imagine how any true differences in neural activity between the two methods may go undetected. Although most fMRI comparisons have been conducted with this between-experiment approach, there have been a few comparisons utilizing a within-subjects design (Duarte, Henson, & Graham, 2008; Vilberg & Rugg, 2007; Yu, Johnson, & Rugg, 2012). The goal of these studies, however, was not to directly compare the two methodologies, but instead to focus on how the amount of recollected information modulates activity within the PPC. While successful in tackling their specific goal, the designs of these studies were not optimal for a direct comparison between remember/know and source tests. First of all, none of these studies directly compared the neural correlates of familiarity between these two methods. Instead, they focused exclusively on recollection-related comparisons. While lately much focus has been made to elucidate the neural correlates of recollection, familiarity-related activity is still far from understood. Therefore, when comparing PPC activations between remember/know and source tests, it is just as important to investigate familiarity-related activity as it is activity related to recollection. Furthermore, none of these studies used the traditional testing methodologies, but instead used variants of the remember/know paradigm to find brain regions that were active during the remember/know task and were additionally modulated by the source task. Therefore, when identifying regions that were sensitive to source recollection, analysis was constrained to regions that were additionally active during recollection in the remember/know task. As a result, no independent measure of objective recollection was/could be reported. Although helpful in highlighting brain regions that are modulated by the *amount* of information recollected (Vilberg & Rugg, 2007; Yu et al., 2012), without an independent measure of source recollection they cannot speak to the apparent convergence between remember/know and source memory tests. In an effort to avoid the limitations of between-subject designs, the current study will have the same group of subjects participate in both a remember/know test and a source memory test. Additionally, the same stimuli (words), scanner protocol, and analysis parameters will be used for both tests. To obtain independent measures of subjective and objective recollection and familiarity, the remember/know test and source test will be taken independent of each other (as opposed to a combined procedure where subjects make a remember/know and/or a source judgment on each trial). The results from these two tests will be directly compared so that potential differences in neural activation may be found, with specific focus on activation within the left PPC. The results of this direct comparison may reveal something important about the assumed equivalence of the remember/know and source memory tests at indexing recollection and familiarity. If neural differences are found between testing methods, then the generally-held assumption that these methods are tapping into functionally equivalent memory processes would need to be readdressed. Additionally, attempts to attribute any particular functional role to PPC activity during memory retrieval would need to take these differences into account.

2. Materials and methods

2.1. Subjects

Twenty-five healthy subjects (7 female) took part in this study. Subjects ranged in age from 19 to 35 years old ($M=24.8$, $SD=4.6$). Data from eight additional subjects were not included in any reported analyses (one due to a failure to complete the experiment in its entirety, two due to an insufficient number of trials of interest <20, and five for excessive movement). All subjects were native English speakers and all except one reported their right hand to be dominant. All subjects gave informed consent as approved by the UCSB Institutional Review Board and were paid for their participation.

2.2. Stimuli

Stimuli consisted of 608 nouns selected using the MRC Psycholinguistic Database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). For counterbalancing purposes, words were pseudorandomly divided into two lists of 304 words each. These lists were matched (as closely as possible) on ratings of concreteness, familiarity, imagability, Kucera Francis written frequency, number of letters and number of syllables. Words were back projected onto a screen at the head of the scanner bore and were visible to the subject by a mirror mounted on the head coil. Words were presented in the center of the screen in black 85-point Times New Roman font against a white background. Stimulus presentation was controlled by a

MacBook Pro laptop running Matlab R2008a version 7.6.0 (The Mathworks Inc., USA), using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

2.3. Procedure

Before entering the scanner, subjects engaged in a short practice session that mimicked what they would experience in the scanner. During this practice session, subjects took a source memory test and a remember/know test. Just prior to the remember/know test, subjects were given explicit instructions and examples of when to make a 'remember' and a 'know' response. These instructions were modified versions from those previously used in the literature (Rajaram, 1993) (see the Appendix for a copy of the test instructions). In an attempt to ensure that these instructions were understood, after completing the practice remember/know test, subjects were asked what specific details were recalled for the items that were given 'remember' responses. Subjects were not allowed to continue with the procedure until the experimenter was convinced that a proper understanding of when to make a 'remember' vs. a 'know' response was achieved. Once in the scanner, the task consisted of four study runs and four test runs. Subjects underwent all four study runs followed shortly by four test runs. During each study run, 76 words were presented one at a time on the screen for 2.5 s followed by a blank screen for .7 s. During two of the study runs, subjects were asked to make a 'Pleasant/Unpleasant' decision about each word, for the other study runs subjects made an 'Abstract/Concrete' decision about each word. Subjects alternated between 'Pleasant/Unpleasant' and 'Abstract/Concrete' runs, with the order pseudo-randomized between subjects. After the fourth study run, an anatomical scan (approximately 9 min long) was collected, during which the subject was allowed to rest. Following this, the subjects began the first of four test runs. Each test run consisted of 152 words (76 old, 76 new), for a total of 608 test words. Each word was displayed on the screen for 2.7 s followed by a blank screen for .5 s. For two test runs, memory was tested using a source memory paradigm. Subjects indicated whether each word had been studied during one of the 'Pleasant/Unpleasant' study runs, during one of the 'Abstract/Concrete' study runs, whether the item was recognized as being part of the study session but the subject did not recall which run the word was presented in ('Don't Know' response), or whether the word was new. For the remaining test runs, subjects engaged in a remember/know paradigm, where subjects made a 'remember' response when recollection occurred, a 'know' response when familiarity was used to make their decision, or a 'new' response. Subjects alternated between 'Remember/Know' and 'Source Memory' runs, with the order pseudo-randomized between subjects. To minimize fatigue, subjects were given a one-min break in the middle of each 12-min test scan. During both the study runs and the test runs, a response scale appeared on the screen below the word to help subjects remember which button mapped onto which response option. Assignment of words to test paradigm and to old/new status was pseudo-randomized between subjects. All responses were made using an MRI-compatible button box held in their right hand. To enable event-related analysis, 41 fixation trials were added to each study run and 79 fixation trials were added to each test run. The order of stimulus events during study and test runs was pre-determined by a genetic algorithm that optimized the design efficiency for the old/new contrast (Wager & Nichols, 2003). Although one could argue that a more effective way to compare the two testing methods would be to integrate remember/know and source decisions within the same run instead of segregating into different runs, we had a specific rationale for avoiding this methodology. Basically, we wanted to replicate how these testing procedures are most commonly used. If we were to introduce a requirement to switch between making remember/know decisions and source decisions on a trial-to-trial basis, then this may involve additional processing that is not normally required during these recognition tests. Particularly since the dorsal parietal area has been shown to be involved with top-down attention (Corbetta & Shulman, 2002), requiring this additional processing of task-switching may modulate the PPC activity, not because of differences between the two tasks, but instead because of this additional procedural step. Therefore, we decided to segregate remember/know and source tests into different runs.

2.4. MRI data acquisition

A 3T Siemens TIM Trio scanner with a standard 12-channel head coil located at the UCSB Brain Imaging Center was used to scan all subjects. Earplugs were provided to minimize noise disturbance and cushions were placed around the subjects' head to minimize movement. A high-resolution anatomical image was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE) with $TR=2.3$ s, $TE=2.98$ ms, and $FA=9^{\circ}$. Each volume was collected with 3-D acquisition and consisted of 160 sagittal slices that were each 1.1 mm thick with 1 mm × 1 mm in-plane resolution. The eight functional runs consisted of a T2*-weighted single shot gradient-echo, echo planar image (EPI) sequence sensitive to the BOLD contrast with $TR=1.6$ s, $TE=30$ ms, and $FA=90^{\circ}$. Volumes were acquired parallel to the AC-PC plane in an interleaved pattern using generalized autocalibrating partially parallel acquisitions (GRAPPA). Each volume consisted of 30 slices that were each 3 mm thick with a 5 mm gap and a 3 mm × 3 mm in-plane resolution. The first four volumes of each functional scan were discarded to allow equilibration of tissue magnetization. Although functional images were collected during the study sessions, these results are beyond the scope of this paper and are not discussed further.

2.5. Preprocessing of MRI data

SPM8 (Wellcome Department of Imagining Neuroscience) was used to perform standard spatial preprocessing of the MRI data. All functional images were realigned to the first volume of the first functional scan using a least squares approach and a 6 parameter (rigid body) spatial transformation. During realignment, images were unwarped in order to minimize variance caused by the susceptibility-by-movement interaction (Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The functional images were then coregistered to the anatomical image using the mean functional image generated during realignment. Next, using standard segmentation procedures, the anatomical T1 image was segmented into images of grey matter, white matter, and cerebral spinal fluid. These images were then spatially normalized to the ICBM Tissue Probabilistic Atlases that come standard in SPM8. The parameters of this transformation were then applied to the functional images, which were re-sampled to 3 mm isotropic voxels. Finally, the normalized images were spatially smoothed using an isotropic Gaussian kernel with an $FWHM=8$ mm.

2.6. Analysis of functional data

SPM8 (Wellcome Department of Imagining Neuroscience) was used for further data analysis. Neural activity at stimulus onset was modeled using a delta (stick) function that was convolved with the canonical hemodynamic response function (HRF). To account for differences in response time (see Section 3.1), reaction time was entered into the model as a parametric modulator of the HRF using a first-order linear transform of the delta function. Data across the four functional runs was concatenated, and session-specific regressors were added into the model. Eleven event-types were modeled in total. Five for the remember/know test: correct rejections, remember hits, know hits, false alarms, and misses and five for the source test: correct rejections, source hits, no source hits, false alarms and misses. 'Source hits' refers to trials in which the item was correctly recognized and was given the correct source attribution. 'No source hits' refers to trials in which the item was correctly recognized but was either given the wrong source attribution or received a 'Don't Know' response. There was an additional event-type of no interest, which was comprised of trials with omitted or multiple responses and trials when instructional information was presented on the screen. The data was high-pass filtered at 128 s and an AR(1) model was used to estimate and correct for non-sphericity of the error covariance (Friston et al., 2002). The general linear model (GLM) was used to obtain parameter estimates of events of interest and subsequent contrast *t*-maps were created for each subject. These contrast maps were then passed on to a second-level random-effects analysis that consisted of testing the contrast against zero using a one-sample *t*-test independently at each voxel across the brain.

2.7. Regions of interest (ROI) analysis

Marsbar (Brett, Anton, Valabreque, and Poline 2002) was used to create and analyze BOLD activation from a priori chosen regions of interest (ROIs). Structural ROIs were determined according to the AAL atlas that is included with the Marsbar software package. These regions were the left superior parietal lobule (BA 7) and the left angular gyrus (BA 39). For these ROIs, the mean percent signal change from baseline within that region was calculated for each event type. Values representing recollection and familiarity (as defined by each test) were then calculated for each subject by subtracting the percent signal change from the appropriate events (e.g. subtracting the percent signal change to know hits from the percent signal change to remember hits for remember/know recollection). These values were then averaged across subjects to obtain a mean percent signal change value for each contrast of interest.

3. Results

3.1. Behavioral results

We calculated overall d′ (memory accuracy) and c (decision criterion) collapsed across recollection and familiarity responses using signal detection analysis. We used a series of paired-samples *t*-tests to compare results between the remember/know test and source memory test. Results revealed no significant difference in d′, $t(24)=.976$, $p=.339$, nor in c, $t(24)=.409$, $p=.686$ between the tests. There was, however, a significant difference in reaction time

Table 1
Overall memory accuracy (d′) and response bias (c) are shown. 'Rec' refers to recollection (either remember hits or source hits) and 'Fam' refers to familiarity (either know hits or no source hits), while 'rt' refers to reaction time.

	d′	c	**Rec rt**[***]	**Fam rt**[***]	**No. of Rec trials**[*]	**No.** of Fam trials
Remember/know	2.11 (.69)	−.07 (.34)	**1.29 (.15)**	**1.58 (.20)**	**76.80 (24.05)**	51.12 (19.95)
Source	2.03 (.81)	−.09 (.37)	**1.69 (.17)**	**1.74 (.18)**	**64.00 (24.62)**	59.88 (17.93)

Mean values are shown with their associated standard deviations in parentheses. Significant differences between the tests are shown in bold font and the significance value is indicated with the associated star(s).

[*] $p < .05$.

[***] $p < .001$.

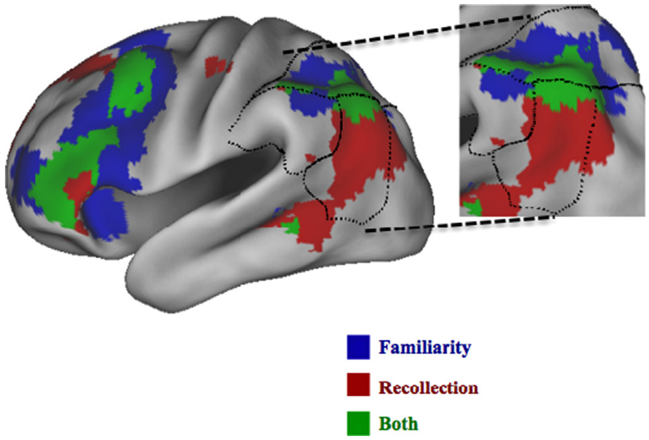

Fig. 1. Brain regions identified by both tests at the group level. Blue indicates regions that were active for familiarity, red for recollection, and green represents regions that were active for both familiarity and recollection. For visualization purpose, results were transformed to the PALS atlas and rendered onto 3D inflated brains using CARET software (Van Essen et al., 2001). Brodmann areas 7, 39, and 40 are indicated with the dotted line (defined by the BA list that comes with the CARET software). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with remember hits ($M=1.29$ s, $SD=.15$ s) being made significantly faster than source hits ($M=1.69$ s, $SD=.17$ s), $t(24)=-14.61$, $p<.001$ and know hits ($M=1.58$ s, $SD=.20$ s) being made significantly faster than no source hits ($M=1.74$ s, $SD=.18$ s), $t(29)=-5.20$, $p<.001$. To ensure that this difference in reaction time was not driving any neural differences that we might find, we added reaction time into our model as a parametric modulator of the delta function used to model the neural activity (see Section 2.6). There was also a significant difference in the amount of recollected trials between the remember/know and source memory tests with a significantly higher number of remember hits ($M=76.8$, $SD=24.0$) than source hits ($M=64.0$, $SD=24.6$), $t(24)=2.27$, $p=.032$. There was no significant difference between the number of know hits and the number of no source hits, $t(24)=-1.648$, $p=.112$. For a summary of the behavioral results, see Table 1.

3.2. *fMRI results*

Although some minor activation was found in the right hemisphere for the contrasts of interest, the following analyses focus mostly on the activation in the left hemisphere. The activity within the left hemisphere was significantly stronger and more consistent than that in the right hemisphere. Additionally, it is activity within the left hemisphere that is consistently reported in the memory retrieval literature. Recollection was operationalized for the remember/know test as the 'Remember hits > Know hits' contrast, and for the source test as the 'Source hits > No Source hits' contrast. Familiarity was operationalized as the 'Know hits > Correct rejections' contrast for the remember/know test and as the 'No Source hits > Correct rejections' contrast for the source test. 'Correct rejections' included only those responses from that test (e.g. correct rejections in the source contrast only included correct rejections from the source test). Unless otherwise specified, voxels were tested at a False Discovery Rate (FDR) adjusted p value of $<.05$ with a voxel extent of 10.

3.2.1. *Brain regions activated by both tests*

Despite which testing method was used, recollection activated relatively ventral PPC regions, while familiarity activated more dorsal PPC regions. Specifically, recollection activated the left angular gyrus (BA 39). Outside of the PPC, regions in the left dorsolateral prefrontal cortex (BA 9 & 46), left ventrolateral prefrontal cortex (BA 45 & 47), regions within the left lateral temporal cortex (BA 22), as well as the posterior cingulate gyrus (BA 23 & 31) were also activated by both tests for recollection. Defined by either test, familiarity activated the area around the intraparietal sulcus (IPS). This activation extended dorsally into the superior parietal lobule (BA 7) and also into the more superior areas of the angular gyrus (BA) 39 and the supramarginal gyrus (BA 40). Extensive familiarity-related activation was also found during both tests in the left dorsolateral prefrontal cortex (BA 9 & 46), left ventrolateral prefrontal cortex (BA 44, 45, & 47), the precuneus (BA 7), and posterior cingulate gyrus (BA 23). See Fig. 1 for a visualization of these common activations. See Table 2 for a list of peak voxel activations associated with these results.

3.2.2. *Results from each test*

In addition to the brain regions that were common to both tasks, some brain regions were uniquely identified depending on what test was used to operationalize recollection and familiarity. Of specific interest to this study, recollection-related activity was only seen in the supramarginal gyrus (BA 40) when it was operationalized by the remember/know test. Familiarity, on the other hand, appeared to activate a larger portion of the superior parietal lobule (BA 7) when operationalized by the source test. See Fig. 2 for the results of the second level of analysis independently for the remember/know test and for the source test. See Table 3 for a list of peak voxel activations associated with these results.

3.2.3. *Direct comparisons between tests*

To specifically compare the results of the two methods, the contrasts that were used to define recollection and familiarity at the first level of analysis for each test were statistically compared. Specifically, activation resulting from each subject's 'Source Hits > No Source Hits' contrast (source recollection) was subtracted from their 'Remember Hits > Know Hits' contrast (remember/know recollection). Similarly, for familiarity, activation resulting from each subject's 'No Source Hits > Correct Rejections' contrast (source familiarity) was subtracted from their 'Know Hits > Correct Rejections' contrast (remember/know familiarity). The resulting difference t-maps (with positive values indicating brain regions that were more active during the remember/know

Table 2
Information from peak voxels found by inclusively masking the 'Remember Hits > Know Hits' and 'Source Hits > No Source Hits' contrasts to represent recollection (a), and the 'Know Hits > Correct Rejections' and 'No Source > Correct Rejections' contrasts to represent familiarity (b). Closest Brodmann areas (BA) labels are provided when possible.

X Y Z coordinates (MNI)	Hemi-sphere	Brain region	BA	*t* Value	Cluster size (voxels)
a. Recollection-related activity					
−9 −43 34	Left	Posterior cingulate/precuneus	31	5.76	672
−3 −58 10	Left	Posterior cingulate	29	5.10	*
−6 −58 28	Left	Precuneus/posterior cingulate	31	4.91	*
−33 14 52	Left	Middle frontal gyrus/superior frontal gyrus	8	5.48	254
−15 59 22	Left	Superior frontal gyrus	10	5.38	*
−6 50 31	Left	Superior frontal gyrus	9	5.14	*
−42 −67 46	Left	Precuneus/angular gyrus	39	5.39	475
−42 −73 31	Left	Lateral occipital cortex/angular gyrus	39	5.32	*
−42 −49 37	Left	Angular gyrus	39	3.86	*
−36 32 −11	Left	Inferior frontal gyrus	47	5.25	198
−24 32 −11	Left	Middle frontal gyrus/inferior frontal gyrus	11	5.18	*
−45 35 7	Left	Inferior frontal gyrus	45	5.02	*
−12 −73 −11	Left	Lingual gyrus	18	4.83	61
−30 −37 −14	Left	Parahippocampal gyrus	36/37	4.70	51
−18 −43 −11	Left	Lingual gyrus/cerebellum		4.56	*
−60 −37 −8	Left	Middle temporal gyrus	21	4.16	34
−57 −52 −8	Left	Middle temporal gyrus	21	4.10	*
24 −37 −11	Right	Lingual gyrus/parahippocampal gyrus	36	4.08	22
18 −88 31	Right	Lateral occipital cortex/cuneus	19	3.82	21
18 8 −11	Right	Putamen		3.62	22
12 11 −5	Right	Caudate/putamen		3.53	*
b. Familiarity-related activity					
−45 −49 46	Left	Supramarginal gyrus/angular gyrus/superior parietal lobule	40/7	6.23	882
−33 −70 52	Left	Superior parietal lobule	7	6.19	*
−9 −70 43	Left	Precuneus	7	4.61	*
−48 17 37	Left	Middle frontal gyrus	9	5.94	1842
−39 50 10	Left	Middle frontal gyrus	10	5.61	*
−6 23 49	Left	Superior frontal gyrus	8	5.56	*
−12 11 1	Left	Caudate		5.59	65
−12 11 10	Left	Caudate		5.21	*
−6 −28 25	Left	Posterior cingulate	23	5.19	140
12 11 1	Right	Caudate		4.53	62
36 20 −2	Right	Insular cortex	47	4.20	101
39 8 58	Right	Middle frontal gyrus	6	3.90	40
45 −58 52	Right	Lateral occipital cortex/angular gyrus/superior parietal lobule	39/7	3.88	69
−3 −25 −2	Left	Thalamus		3.56	10
−3 −25 −11	Left	Brainstem		3.35	*
48 29 37	Right	Middle frontal gyrus	9	3.49	14

* Denotes that the peak voxel is part of the cluster in the row(s) directly above it.

test compared to the source test) were then brought up to the second-level of analysis and compared against zero using a one-sample *t*-test at each voxel across the brain. These results are described below and are shown in Fig. 3a and b. Since recollection is defined by subtracting out activity to familiarity hits, we wanted to ensure that any neural difference observed between recollection was truly due to differences in recollected hits, and not to differences to familiarity hits. Therefore, at the first-level of analysis, a 'Remember Hits > Source Hits' contrast was generated for each subject. The same argument holds for familiarity. To ensure that the neural differences observed were not due to differences to correct rejections, a 'Know Hits > No Source Hits' contrast was generated for each subject. The resulting *t*-maps were brought up to the second level of analysis and compared against zero using a one-sample *t*-test at each voxel across the brain. These results are described below and are shown in Fig. 3c and d. Results from both of these analyses show that the ventral region of the left PPC (specifically the supramarginal gyrus) was significantly more active when recollection was indexed by the remember/know test compared to when it was indexed by the source test. Conversely, the dorsal PPC region was significantly more active when familiarity was indexed by the source test compared to when it was indexed by the remember/know test.

3.2.4. Regions of interest (ROI) analysis

Percent signal change from (implicit) baseline was calculated for each event type for each subject. To calculate the percent signal change associated with recollection and familiarity, the following subtractions were performed: 'Remember hits – Know hits', 'Source hits – No Source hits', 'Know hits – Correct Rejections', and 'No Source hits – Correct Rejections'. These differences represent the percent signal change for remember/know recollection, source recollection, remember/know familiarity, and source familiarity respectively. Fig. 4 shows the mean (across subjects) percent signal change for these events calculated within the left angular gyrus (BA 39) and left superior parietal lobule (BA 7) for recollection and familiarity respectively. Although the left angular gyrus was active for recollection during both tests, results from a paired samples *t*-test revealed a significant difference in the mean percent signal change between recollection indexed by the remember/know test (M=.18, SD=.12) and recollection indexed by the source test (M=.09, SD=.08), $t(24)$=3.88, $p < .001$, with the remember/know test significantly activating this region more than the source test. Similarly, while both tests activated the superior parietal lobule during familiarity, a paired samples *t*-test revealed a significant difference between familiarity as defined by the remember/know test (M=.05, SD=.10) and by the source test

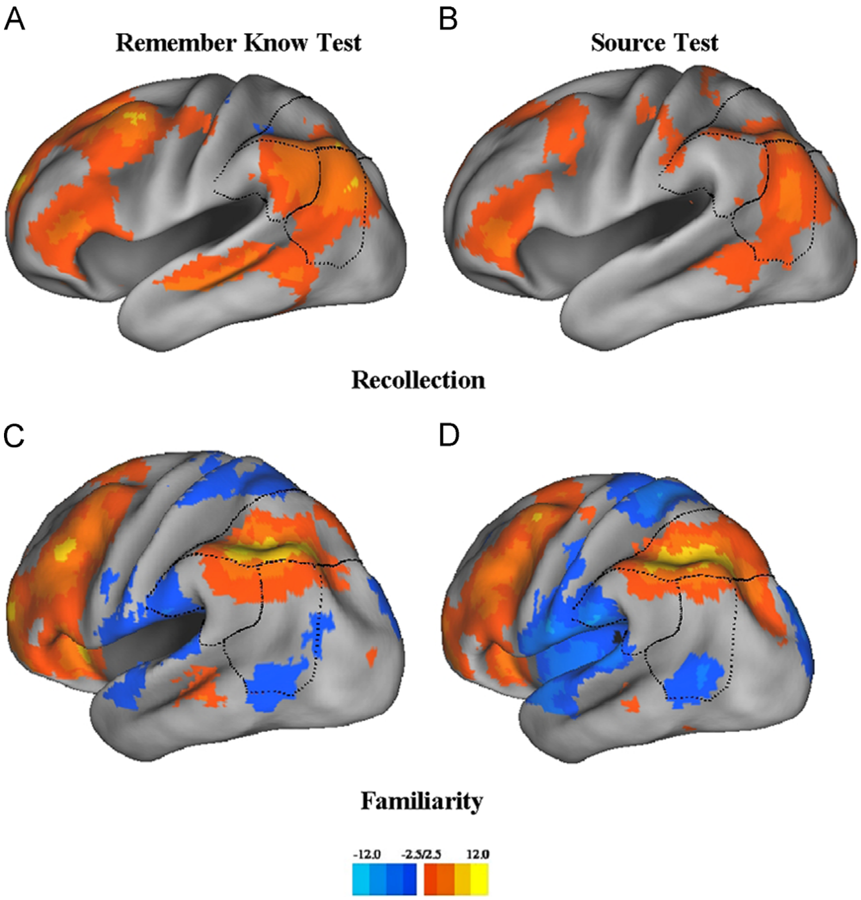

Fig. 2. Group-level results of Remember Hits > Know Hits (a), Source Hits > No Source Hits (b), Know Hits > Correct Rejections (c), and No Source Hits > Correct Rejections (d) For optimal visualization recollection is presented on a lateral view of the brain and familiarity is presented at a slightly more dorsal view.

(M=.13, SD=.14), $t(24)=-3.01$, p=.006, with the source test significantly activating this region more than the remember/know test.

3.2.5. *Relationship between dorsal and ventral PPC activity differences*

Differences in activation levels between testing methods were compared between the dorsal and ventral PPC regions within-subjects. Specifically, differences in the percent signal change between the two tasks during recollection within the superior parietal lobule (BA 7) were used to predict percent signal change differences during recollection within the inferior parietal lobule (BA 39 and BA 40). For each subject, percent signal change (calculated from the ROI analysis) for remember/know recollection was subtracted from the percent signal change for source recollection. This was performed separately for the left superior parietal lobule (BA 7), the left angular gyrus (BA 39), and the left supramarginal gyrus (BA 40). These difference values were then correlated within-subject to see how well one could predict changes in ventral PPC activity (BA 39 or BA 40) between tasks from changes in the same subject's difference in dorsal PPC activity (BA 7) between tasks. Results revealed a significant positive correlation between activity differences in the superior parietal lobule and activity differences in both ventral PPC sub-regions, angular gyrus, $r(23)=.58$, p=.003 and supramarginal gyrus $r(23)=.66$, $p<.001$. See Fig. 5 for scatterplots representing this relationship.

4. Discussion

There are two common strategies for identifying the neural correlates of recollection and familiarity. One is the remember/know test, which relies on the subject's ability to correctly classify the type of retrieval used to recognize the item. The other strategy involves probing source memory, requiring the subject to qualify their recognition with the retrieval of a specific piece of contextual information predetermined by the experimenter. Although both testing methods has its own set of limitations, previous research has found a convergence within the left posterior parietal cortex (PPC) as to the general brain regions that become active during retrieval. Familiarity has been shown to activate relatively dorsal regions, while recollection activates more ventral regions within this cortical area (Ciaramelli et al., 2008; Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). The results from the current study are in agreement with this general finding. Activation relating to familiarity occurred around the left intraparietal sulcus (IPS) and extended well into the superior parietal lobule (SPL) during both the remember/know and source memory tests. Similarly, regardless of what test was used, recollection-related activity occurred within the ventral PPC regions, activating the inferior parietal lobule (IPL), with overlap within the angular gyrus. What has yet to be examined in the fMRI literature is a direct comparison between these two strategies of separating recollection and familiarity. While evidence from ERP studies (Rugg et al., 1998; Mark & Rugg, 1998) shows a similar parietal 'old/new' effect between the two methods, a much more fine-grained dissociation between PPC sub-regions cannot be determined

Table 3
Information from peak voxels for Remember Hits > Know Hits (a), Source Hits > No Source Hits (b), Know Hits > Correct Rejections (c), and No Source Hits > Correct Rejections (d) contrasts from the group analysis. Closest Brodmann areas (BA) labels are provided when possible.

***X Y Z* coordinates (MNI)**	**Hemi-sphere**	**Brain region**	**BA**	***t* Value**	**Cluster size (voxels)**
a. Remember Hits > Know Hits					
−9 −43 34	Left	Posterior cingulate gyrus	31	8.61	21030
−30 −34 −14	Left	Parahippocampal gyrus	36	6.73	*
−18 59 22	Left	Superior frontal gyrus	9/46	7.94	20830
−36 8 52	Left	Middle frontal gyrus	6	7.93	*
−42 −67 46	Left	Lateral occipital cortex/angular gyrus	19/39	7.64	11170
−54 −61 37	Left	Supramarginal gyrus/angular gyrus	40/39	6.95	*
−36 32 −11	Left	Inferior frontal gyrus	47	7.29	344
−57 −28 −8	Left	Middle temporal gyrus	21	7.28	434
30 −43 −8	Right	Parahippocampal gyrus	36	6.64	147
51 −70 22	Right	Angular gyrus/lateral occipital cortex	39/19	5.63	57
69 −25 4	Right	Superior temporal gyrus	22	5.32	164
54 35 4	Right	Inferior frontal gyrus	45/46	5.20	59
24 −82 40	Right	Precuneus/cuneus/lateral occipital cortex	19	4.79	79
21 −88 31	Right	Cuneus	18/19	4.55	*
−45 −16 49	Left	Postcentral gyrus	3	4.49	24
b. Source Hits > No Source Hits					
−6 −58 28	Left	Posterior cingulate gyrus/precuneus	31	9.08	958
−45 −67 19	Left	Middle temporal gyrus/lateral occipital cortex	37/19	5.98	490
−39 −67 46	Left	Lateral occipital cortex/angular gyrus	19/39	5.84	*
−45 44 7	Left	Middle frontal gyrus/inferior frontal gyrus	10/46	5.97	292
−9 56 34	Left	Superior frontal gyrus	9	5.35	238
36 −31 −11	Right	Parahippocampal gyrus/hippocampus	37	5.02	86
3 −1 31	Right	Anterior cingulate gyrus	24	4.80	27
21 −1 −11	Right	Amygdala		3.75	33
−24 −37 −17	Left	Fusiform cortex	20	4.53	47
−18 −40 −8	Left	Parahippocampal gyrus	36	4.12	*
39 −79 1	Right	Lateral occipital cortex	19	4.44	51
18 −49 40	Right	Precuneus	31	4.37	11
36 −31 52	Right	Postcentral gyrus	3	4.28	18
−12 −79 −2	Left	Lingual gyrus	18	4.25	56
c. Know Hits > Correct Rejections					
−45 −49 46	Left	Superior parietal lobule/supramarginal gyrus	7/40	10.04	933
−9 −70 43	Left	Precuneus	7	5.92	*
−48 17 37	Left	Middle frontal gyrus	8/9	9.12	26220
−39 50 10	Left	Middle frontal gyrus	10	8.20	*
−6 23 49	Left	Superior frontal gyrus	8	8.05	*
−3 −16 31	Left	Anterior cingulate gyrus	23	6.16	250
−60 −43 −5	Left	Middle temporal gyrus	20/21	5.25	73
36 20 −2	Right	Insula	47/13	5.17	141
42 47 16	Right	Middle frontal gyrus	10	4.77	59
45 −58 52	Right	Superior parietal lobule/angular gyrus	7/39	4.63	117
48 −49 43	Right	Angular gyrus/supramarginal gyrus	39/40	4.56	*
d. No Source Hits > Correct Rejections					
36 −73 40	Right	Precuneus	19	9.86	18730
−30 −67 49	Left	Precuneus/lateral occipital cortex	19	8.88	*
−45 −49 46	Left	Angular gyrus/supramarginal gyrus/superior parietal lobule	39/40/7	8.86	*
−48 11 37	Left	Middle frontal gyrus	9	7.74	21140
36 5 61	Right	Middle frontal gyrus	6	6.79	186
−3 −28 31	Left	Posterior cingulate gyrus	23	6.78	151
30 23 −5	Right	Insula	13	5.73	121
−18 −79 −11	Left	Fusiform gyrus	18/19	5.06	64
51 32 28	Right	Middle frontal gyrus	9	4.82	70

[*] Denotes that the peak voxel is part of the cluster in the row(s) directly above it.

with this technique. For this, the superior spatial resolution granted by fMRI techniques should be taken advantage of. While there have been some fMRI studies investigating recollection and familiarity using both methods, these comparisons have been less than optimal (as previously explained). This type of direct and adequate comparison could be informative, particularly within the left PPC, where much debate has centered on the functionality of neural activity that is consistently observed during memory retrieval. Although both methods are ostensibly signaling the experience of the same memory states (i.e. recollection and familiarity), the specific memory content retrieved, as well as the cognitive demands associated with this retrieval, may vary between the two procedures. While remember responses can be made based on the retrieval of *any* contextual information, source responses are dependent upon the retrieval of *specific* contextual information. As described by Ciaramelli et al. (2008), this information may not be the first that pops into the subject's mind, and therefore, may have to be strategically searched for. This often effortful search may require additional resources from ancillary cortical areas that may control functions such as top-down attention (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Cabeza, Ciaramelli, & Moscovitch, 2012; Ciaramelli et al., 2008) or the orienting towards such types of associative retrieval (Dobbins & Wagner, 2005; O'Connor, Hans, & Dobbins, 2010; Jaeger, Konkel, & Dobbins, 2013).

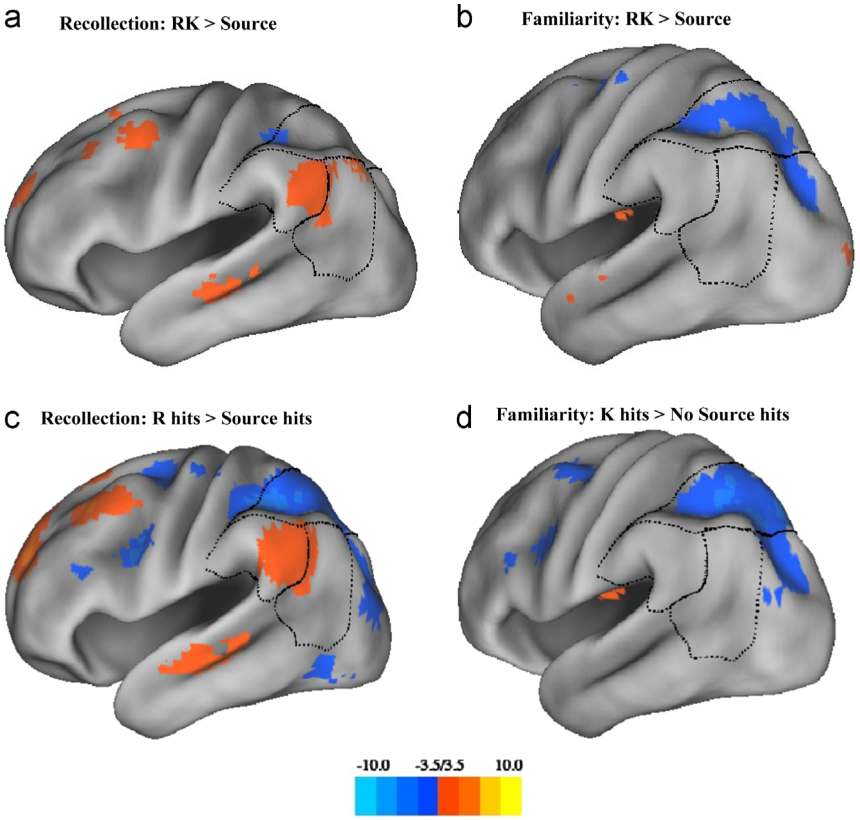

Fig. 3. Group-results ($p < .001$, voxel extent = 10) for Recollection (a) and (c) and Familiarity (b) and (d). Contrasts show the difference between the remember/know and source tasks for recollection (a) and familiarity (b). Also shown are the contrasts between 'remember hits > source hits' (c) and 'know hits > no source hits' (d).

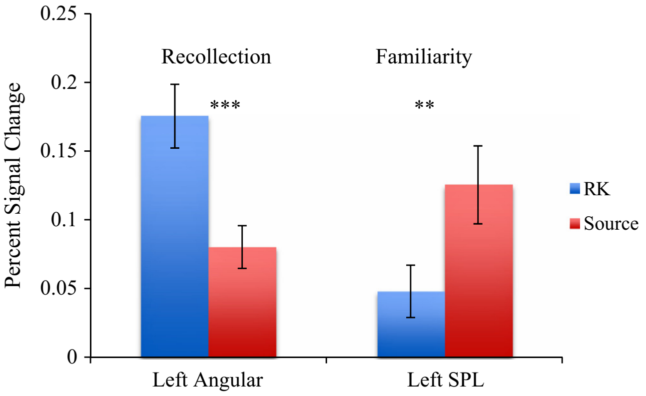

Fig. 4. Mean (across subjects) percent signal change for recollection and familiarity. On the left is the change in signal in the left angular gyrus (BA 39) for remember hits (blue) and for source hits (red). On the right is the change in signal in the left superior parietal lobule (BA 7) for know hits (blue) and no source hits (red). Error bars represent the standard error of the mean. Significance values are indicated with the associated number of stars ($p < .01 =$ **, $p < .001 =$ ***). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This may be why some previous studies have shown additional activity in posterior parietal and prefrontal cortices when comparing source judgments to remember responses (Duarte, Ranganath, & Knight, 2005; Ciaramelli et al., 2008). On the other hand, remember responses are not as restricted as to what specific detail constitutes recollection. This may put less demand on the top-down attentional system, freeing up resources to allow for the bottom-up attentional system to act as a circuit-breaker, reorienting internal attention towards retrieved contextual information that may not be relevant during the source test. Such information may include autobiographical memories (e.g. previous memories that the subject associated

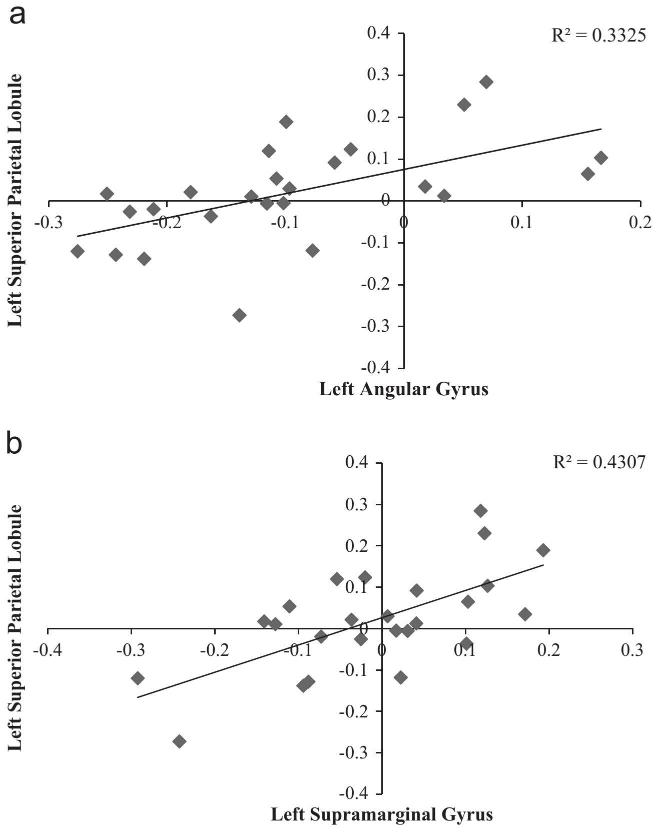

Fig. 5. Relationship between the difference in superior parietal lobule activity (BA 7) between the two tasks (Source recollection—RK recollection) and the difference in the angular gyrus (a) (BA 39) and supramarginal gyrus (b) (BA 40) activity between the two tasks.

with the particular word) or self-referential processing (e.g. "*I* remember what *I* was thinking about when *I* saw that word on the study list") that would be sufficient to make a remember but not a source response. Evidence to support this idea that activity within the PPC, particularly the ventral regions, can be modulated by the relevancy of mnemonic information has been presented previously (Elman & Shimamura, 2011). If different patterns of neural activations are found depending on the testing procedure used to probe recollection and familiarity, then that would provide evidence that these divergent brain regions are reflecting some cognitive process (es) that are specific to the demands of the task. If instead, similar activations are found using both testing procedures, then that would provide evidence to support the previous assumption that these two methods are functionally equivalent at separating the neural correlates of recollection and familiarity.

4.1. *Summary of current findings*

The current design allowed for the direct comparison of the neural correlates of recollection and familiarity as operationalized by the remember/know and source memory procedures. Results revealed large areas of convergence, namely familiarity-related activity within the superior parietal lobule and recollection-related activity within the angular gyrus. In addition to this overlap, striking divergent activations were also observed between the testing methods. Within the left PPC, the magnitude of activation significantly differed between testing method. Although both tests revealed familiarity-related activity within the SPL, this activity was greater when familiarity was indexed by the source test compared to when it was indexed by the remember/know test. While both tests showed recollection-related activity within the left IPL, specifically in the left angular gyrus, this activation was significantly greater when recollection was probed by the remember/know test compared to the source test (as evidenced in the ROI analysis). Beyond differences in magnitude, the extent of activity also varied between testing procedure. When familiarity was assessed using the source test, activation spread more dorsally, covering a greater extent of the left SPL. When the remember/know paradigm was used, familiarity-related activation spread slightly more ventrally into the superior regions of the left supramarginal and angular gyri. Turning to activity related to recollection, the most striking regional differences were observed. While source memory recollection was confined to the more posterior portion of the IPL, namely the angular gyrus, remember/know recollection extended well into the supramarginal gyrus and into the temporo-parietal junction (TPJ). Additionally, the difference in activation between testing methods observed in the dorsal PPC regions was shown to be positively related to the difference in activation observed in the ventral PPC regions within subjects. In other words, the more a particular subject's dorsal PPC activity varied between testing method, the more that subject's *ventral* PPC activity also varied between testing method.

4.2. *Relation to previous findings*

Previous research has found a similar difference in the magnitude of recollection and familiarity-related activations between the remember/know and source test procedures. In a meta-analysis, Ciaramelli et al. (2008) compared the results from nine experiments using the remember/know paradigm with 11 experiments using a source memory test. Results showed that the left SPL was associated with higher levels of activity when using source memory compared to the remember/know procedure. Conversely, regions within the left IPL were more strongly activated by experiments that used the remember/know test compared to those using tests of source memory. The current experiment replicated these findings within the same group of subjects. This finding is important because it shows that this differential activation is still present even when confounding variables such as differences in stimuli, analysis technique, scanner protocols, specific subjects tested, etc. are held constant. Thus, this difference is most likely truly attributable to differences in task demands and not to differences in extraneous variables that were previously free to vary between testing procedure. Turning to differences in the extent of activity, this difference was most noteworthy in the activity associated with recollection. While both tests activated the angular gyrus, only the remember/know test additionally activated the supramarginal gyrus. In these analyses, a more lenient threshold of uncorrected $p<.001$ was used in these direct comparisons because the analyses were testing the significant difference between differences. Although a more liberal threshold was used, the specific PPC area of significant activity (the left supramarginal gyrus) was precisely the area predicted by the previous analyses that used a more conservative threshold. In addition to this, the extent of activity was relatively large (257 voxels). Therefore we feel confident that the result of this analysis is not merely a reflection of spurious activity. Although it is unclear why only subjective measures of recollection activated this anterior region of the IPL, there is some literature that supports this finding. Using the combined remember/know & source memory paradigm, Yu et al. (2012) found that the angular gyrus was active for recollection using either testing method, but a cluster within the supramarginal gyrus/TPJ was active for recollection only as indexed by the remember/know test. The results of the current experiment replicate these findings and more importantly show that these results can be found when using the traditional remember/know and source memory testing procedures, which allow recollection and familiarity to be operationalized independently by both testing methods. This finding also goes along with research suggesting that different sub-regions of the IPL may be responsible for different functional roles during memory retrieval. Anterior IPL regions have been suggested to play a role in cognitive processes that aid in memory retrieval (such as directing attention or planning motor movements), while more posterior regions have been suggested to be playing a more direct role in temporarily storing memory content (Caspers et al., 2011; Daselaar, Huijbers, Eklund, Moscovitch, & Cabeza, 2013; Hutchinson et al., 2009; Nelson et al., 2010). For instance, Hutchinson et al. (2009) performed a meta-analysis comparing regions within the left PPC that respond to manipulations of bottom-up attention to those that respond to successful memory retrieval. Results showed that activity related to reflexive attention occurs in anterior IPL regions (supramarginal gyrus/TPJ) while retrieval effects were located within the posterior IPL regions (angular gyrus). Structural connectivity differences also offer support for dissociations within anterior and posterior IPL regions. In a diffusion tensor imaging (DTI) study, Caspers et al. (2011) found that connectivity patterns shifted gradually as one moved from anterior IPL regions to posterior IPL regions. Whereas anterior regions highlighted connections to somatosensory and superior parietal areas, more posterior IPL regions were predominantly connected to the temporal lobe. Functional connectivity techniques have also discovered differences between the anterior and posterior IPL regions. Using a resting-state functional connectivity analysis, Daselaar et al. (2013) found a supramarginal gyrus seed region to be functionally connected with putative attention regions within the ventral prefrontal cortex, while the angular gyrus seed was functionally connected to the hippocampus. Nelson et al. (2010) developed and implemented a parcellation scheme that integrated data from resting-state functional connectivity and fMRI to define functionally different sub-regions with the left PPC. Their meta-analysis of eight studies revealed that retrieval-related activity occurred in the posterior IPL regions, including the angular gyrus. Regions in the anterior portions of the PPC, including the supramarginal gyrus, did not show this retrieval-related activity. Cohen et al. (2008) defined borders between putative functional areas based on abrupt changes in global patterns of functional connectivity. They highlight a supramarginal/angular gyrus distinction as the prime example of a strong border of rapid change. Although there is some debate as to whether this anterior/posterior distinction represents a 'fractional view' (Nelson, McDermott, & Petersen, 2012) or an 'overarching view' (Cabeza et al., 2012), there seems to be somewhat of a consensus that some functional difference (possibly between bottom-up attention and memory retrieval) exists between anterior and posterior sub-regions within the left ventral PPC.

4.3. Relation to current theories of PPC function during memory retrieval

Within the dorsal areas of the PPC, there is a relative consensus that familiarity-related activations are reflecting some cognitive process that is *related to* memory retrieval as opposed to reflecting the *results of* memory retrieval. Some of the processes suggested for this area include: a modulation of top-down attention (Cabeza, 2008; Cabeza et al., 2008 , 2012; Ciaramelli et al., 2008), retrieval orienting (Dobbins & Wagner, 2005; O'Connor et al., 2010; Jaeger et al., 2013), and the conservativeness of the subject (Aminoff et al., 2014). Although all three of these cognitive processes should occur during both the remember/know and source memory tests, one could argue that these processes may be in higher demand during the source memory test. While the results from this study cannot directly compare these competing theories, they go along with the general idea that source decisions as compared to remember/know decisions may result in additional cognitive processing. For instance, the very act of attempting to retrieve a specific contextual detail (as is required in the source test) has been shown to increase activity within the PPC. Specifically, simply orienting towards this type of source-related retrieval, even when it is not successful, has led to increased activity levels in the dorsal PPC regions, compared to when standard recognition is attempted (Dobbins & Wagner, 2005; Dobbins, Rice, Wagner, & Schacter, 2003). Additionally, as previously explained, source memory responses, as compared to remember/know decisions, may require an increase in top-down attention in order to navigate through the contents of memory to find that specific piece of contextual information. Numerous studies have shown that activity levels within the dorsal PPC increase as the difficulty in memory search increases (Cabeza, 2008; Ciaramelli et al., 2008; Kim & Cabeza, 2007; Henson, Hornberger, & Rugg, 2005). In the current study, hits made during the source task took a significantly longer amount of time to make compared to hits made during the remember/know task (both for recollection and familiarity) suggesting that some additional cognitive processing was occurring during this test. Although we can't make claims as to what specific cognitive process(es) may be occurring during the source test, the fact that a greater level of activity was found in the dorsal PPC regions is consistent with the idea that *some* additional processing is occurring in this test that is not occurring during the remember/know test. Although the focus of this paper is on the parietal lobe, it is interesting to note that familiarity-related activity extended more posteriorly into the occipital lobe when it was defined by the source test as compared to the remember/know test. This finding is consistent with research showing increased occipital activity during source compared to standard item recognition (Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001; Cycowicz, Friedman, & Snodgrass, 2001; Suzuki, Tsukiura, Matsue, Yamadori, & Fujii, 2005). It is somewhat unclear why this region was more sensitive to source familiarity than remember/know familiarity in the current study. One explanation may be that subjects were trying to re-envision the encoding event during the source task. During the encoding scans, the words 'Abstract' and 'Concrete' or 'Pleasant' and 'Unpleasant' were on the screen below each word to help subjects remember what their response choices were. It is possible that during retrieval in the source test subjects may have been trying to re-imagine this visual scene. Such imagery may have resulted in an increase in visual processing, leading to the observed increase in occipital activity. However, such speculation is post hoc and in need of further research. Unlike the dorsal PPC regions, there is quite a debate in the literature as to whether activity within the ventral PPC regions reflect cognitive processes *related* to memory retrieval or whether these activations represent the retrieved memory content itself. The cognitive process that has garnered the most support is the capture of bottom-up attention. According to the dual-attentional process theory, strong memories engage the exogenous attention system, serving to shift one's focus towards the retrieved memory content, particularly when that content is salient or unexpected (Cabeza, 2008; Cabeza et al., 2008, 2012; Ciaramelli et al., 2008). This idea stems from work in the perception literature, where a dissociation between top-down and bottom-up attention has been found between dorsal and ventral PPC regions respectively (Corbetta & Shulman, 2002). Dual-attentional process theory simply extends this idea into the realm of memory. Proponents of this region holding memory content (i.e. the output buffer hypothesis), on the other hand, advocate that this region is playing a similar role to working memory regions in the prefrontal cortex (Baddeley, 2000), temporarily storing episodic memory content online until a decision can be made (Vilberg & Rugg, 2008). Similarly, it has also been argued that the ventral PPC is acting as a convergence zone for disparate neocortical regions (Shimamura, 2011). Regardless of which theory is used to describe the differences in activation observed in the current experiment, the fact that these differences exist is an important finding for the field of memory research, which currently uses the remember/know and source memory tests as equivalent methods of separating familiarity and recollection. These differences are in direct contrast with the belief that results from the remember/know and source tests are "neurally and functionally equivalent" (Rugg et al., 1998, p. 47), and are "indistinguishable" (Mark & Rugg, 1998, p. 861) from and "near identical to" (Yonelinas & Jacoby, 1995, p. 637) each other. In the current study, even though both tests activated the angular gyrus during recollection, the remember/know test did so to a greater magnitude than the source test. Whichever theory is used to explain the functional role of the PPC during memory retrieval, it must take these differences into account. If attempting to explain this differential activation in terms of the output buffer hypothesis, one might conclude that more memory content is being retrieved via the remember/know process. This would make sense since remember/know recollection is not as constrained in the way it is operationalized compared to source recollection. During remember/know recollection the subject may be retrieving lots of recollected content that would not be relevant to the source task. During the source task, this buffered memory content may be limited to only that which is task-relevant, i.e. the decision made during encoding of the word (abstract/concrete or pleasant/unpleasant). Therefore, even though the dorsal PPC regions may be responsible for conducting the constrained memory search, the ventral PPC regions would also be modulated by the goals of the task, and only be buffering task-relevant memory content that is the product of the memory search. Similar modulations of ventral PPC activity have been shown in the attention literature, where activity in this region is not activated by all salient stimuli, but instead only to those that are perceptually similar to the target (for a review, see Corbetta, Patel, & Shulman, 2008). This type of ventral PPC modulation has more recently been extended to the domain of memory retrieval, showing that activity is modulated by the mnemonic relevancy to the current task (Elman & Shimamura, 2011). Another possibility is that this region may not actually be reflecting the products of retrieval, but instead is representing some cognitive process that is more heavily engaged during remember/know recollection compared to source recollection. As explained previously, remember/know recollection may cause the subject to orient attention towards retrieved memory content that is more autobiographical in nature. Berryhill, Phuong, Cabeza, and Olson (2007) showed that patients with bilateral damage to the angular gyrus showed severely impaired free recall of autobiographical-based details compared to controls. Along these lines, others have shown a relationship between posterior parietal damage and deficits in the subjective experience of recollection, specifically in terms of subjective vividness, robustness, and confidence (Ally, Simons, McKeever, Peers, & Budson, 2008; Davidson et al., 2008) even when source recollection remained intact (Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Davidson et al., 2008). It may be that activity within the ventral parietal cortex is related to this self-referential state of mind. In other words, ventral PPC activity may be what makes the memories feel personally relevant to (or belonging to) the individual. The study by Davidson et al. (2008) specifically describes a patient SM who spontaneously reported that in real-life she “often felt like she did not know where her memories had come from” (p. 1751). Collectively, this data suggests that the ventral parietal cortex may be involved with constructing a subjective sense of ownership of one's memories, or with associating an egocentric or self-oriented state of mind to accompany retrieved memories. Of course, it could also be the case that this activity is not reflecting this subjective experience, but instead is redirecting attention *towards* this type of processing. While these types of cognitive processes (self-referential processing, subjective experience of retrieved information, or the reorienting of attention towards these processes) could be engaged in both types of recollection, it may be relied upon more during remember/know recollection than source recollection. Of course, these two explanations need not be thought of as mutually exclusive. It's certainly possible (particularly given the heterogeneity of the parietal cortex) that the activity seen in the angular gyrus may not only represent memory content, as in an episodic memory buffer account, *but also* be a reflection of additional cognitive processing that can accompany recollection (such as bottom-up attention). More research with the specific goal of teasing these two hypotheses apart using more precise segregations of this complex cortical area will be needed to resolve differences between these competing, but not mutually exclusive, hypotheses. While both tests activated the angular gyrus, only recollection as indexed by the remember/know test additionally activated the supramarginal gyrus portion of the IPL. The supramarginal gyrus was not activated during the source test even when the threshold was significantly lowered, suggesting that this differential activation was not simply a matter of conservative thresholding. This divergence, like that of the angular gyrus, suggests that this activity reflects either a difference in memory content retrieved or a difference in a cognitive process (or processes) required to probe recollection. A promising candidate cognitive process for this area is the capture of bottom-up attention. As previously described, remember/know recollection can be identified by whatever contextual information first ‘pops’ into mind, while source memory responses are restricted to the retrieval of a specific piece of contextual information. This restriction placed on source memory recollection may discourage the subject from engaging this reflexive attentional system since it may often shift internal focus onto retrieved information that is irrelevant to the task. Such gating of the reflexive attentional system has been documented in numerous perceptual tasks (Folk, Remington, & Johnston, 1992; Theeuwes & Burger, 1998; Hillstrom & Yantis, 1994) and even within memory tasks (Elman & Shimamura, 2011), suggesting that the salience of an object is strongly influenced by its behavioral relevance and is not solely a function of its distinctive features. Therefore, the subject may employ a more top-down attentional network during the source task so that the desired piece of contextual information required for a recollected response can be strategically searched for. This may explain why even in the comparison of recollected responses, the *dorsal* PPC areas were more strongly activated during the source compared to the remember/know test. The remember/know test is much more inclusive in what information can qualify as a recollective experience. With a broader definition of a recollected response, one may benefit from engaging the bottom-up attention network, allowing the presence of any contextual information to avert attention towards the retrieved content. Response time differences offer some additional support for this explanation, with source memory hits being made significantly slower than remember hits. If subjects were employing a more bottom-up attentional network, as opposed to a more top-down attentional system, during the remember/know test, it would make sense that these responses would be made faster. While bottom-up attention is an intriguing potential cognitive process for this anterior IPL region to be playing during memory retrieval, the results from the current study are far from conclusive and leave open the possibility of several other cognitive processes. An interesting result from the current experiment is that the difference in dorsal PPC activity between tasks was positively correlated with the difference in ventral PPC activation levels within subjects. This result is interesting in that it was somewhat unexpected. If any relationship were detected between the dorsal and ventral PPC regions, it was expected to be a negative, not a positive, relationship. If the ventral PPC regions are acting as a buffer, and if the dorsal regions are helping to constrain the memory search more during the source than the remember/know task, then one would expect the amount of memory content that is retrieved (and therefore buffered) to be *less* during the source task compared to the remember/know task. While clearly not in line with the output buffer hypothesis, this result does not fit well with an attention account either, at least at first glance. One way of thinking about the top-down and bottom-up attention systems is that they act in an antagonistic way, meaning that the more one is engaged, the less the other is engaged. However, some have argued that the difference between the attentional functions of dorsal and ventral PPC regions is not a sharp dichotomy, but is instead a graded difference (Cabeza, 2008). Specifically, dorsal regions have shown some sensitivity to the presentation of infrequent events, which suggests that this region is also affected by bottom-up attentional processes. Additionally, the ventral regions have been shown to be modulated by task relevancy, suggesting it is affected by top-down goal-directed processes (for a review, see Corbetta et al., 2008). If this viewpoint is taken, then an increase in top-down attention centers may also result in an increase in bottom-up attention centers, and the two systems need not be thought of as in direct competition. Therefore, the results from the current experiment may not be in contrast to an attentional account of the PPC. Even if one does not agree with an attentional explanation of this relationship between dorsal and ventral PPC regions, the positive correlation found between these areas suggests that *some* cognitive process is being engaged differently between the two testing procedures. Whatever theoretical account is used to explain PPC activity during memory retrieval must be able to explain this positive relationship between dorsal and ventral activity differences between the tasks.

4.4. Relation to patient data

One of the most intriguing aspects of the parietal activity often observed during memory retrieval is its paradoxical relationship with studies involving patients with parietal lobe damage. With such robust and consistent activity observed in this region, one would think that severe, deleterious effects (such as those seen in medial temporal lobe patients) would be observed in patients with damage to this area. However, there is a curious lack of (obvious) memory impairment associated with parietal patients, although more recent research shows that there may indeed be more subtle effects. While no extensive amnesia-like symptoms have been reported, some researchers have found a lack of richness, subjective experience, and overall confidence with recollected memories in parietal lobe patients. As previously described, studies with parietal lobe patients have reported significantly lower confidence in their memories despite performing as well as controls (Ally et al., 2008; Simons et al., 2010) and have reported specific impairments with remember/know estimates of recollection while showing no impairment on source recollection (Davidson et al., 2008). Authors of these studies concluded that the parietal lobe may have something to do with processing the subjective conscious experience of retrieved memories. The study by Berryhill et al. (2007) that was previously mentioned is also in agreement with this finding, however they interpreted the results a bit differently. They described ventral parietal lobe patients who experienced recollections that lacked richness and specificity when they were asked to freely recall memories. Curiously, these same patients were able to access these memories when they were explicitly probed about them. This led the authors to explain their results in terms of the dual attentional processes hypothesis. Their reasoning is as follows: the damage in these patients was relatively limited to the ventral PPC regions, thus according to the dual attentional processes hypothesis, only bottom-up attention should be affected with top-down allocation of attention left relatively intact. Since the patients were able to use explicit memory cues to retrieve memory content (ostensibly using top-down attention) but were unable to retrieve those same memories spontaneously via free recall (ostensibly using bottom-up attention), they believe their results were in line with this hypothesis. Although it is difficult to localize brain damage to a specific region, the patient data reported seemed to affect the ventral PPC regions more consistently than the dorsal regions. To the extent that this is true, this patient data is relatively in agreement with the results of the current study. Although both remember/know and source recollection activated the ventral PPC regions, the extent of this activation was much greater in the remember/know paradigm. Regardless of what particular cognitive role the ventral PPC is playing during memory retrieval, the current study shows that remember/know recollection relies more heavily on this activity than source recollection. Therefore it makes sense that parietal lobe patients who have damage to this area would show more deficits in remember/know compared to source recollection.

4.5. *Future research*

While the posterior parietal lobe has received a lot of attention recently in the field of memory retrieval, the exact functional role this area (particularly the ventral portion) is playing is clearly still up for debate. More targeted fMRI studies may shed light on the theories that have been proposed so far. However, a more fruitful endeavor may be to capitalize on the relatively non-invasive technique of transcranial direct current stimulation (tdcs). Neurostimulation techniques such as tdcs have the benefit of possibly determining a causal role for brain activity which cannot be afforded by imaging techniques such as fMRI. While lesion data can also determine cause-and-effect relationships, it is often a messy process, with multiple brain regions besides the ones of interest being affected. While neurostimulation techniques have shown to be advantageous in studies of working memory (Zaehle, Sandmann, Thorne, Jäncke, & Hermann, 2011; Andrews, Hoy, Enticott, Daskalakis, & Fitzgerald, 2011), it has not been explored much in terms of long-term memory (but see Ferrucci et al., 2008 for its use with Alzheimer's patients). In order to claim that the PPC activations consistently observed with fMRI studies of memory retrieval are not merely epiphenomenal, a direct causal role for this activity must first be established. Until then, any speculation of functional importance of the parietal cortex during memory retrieval must be interpreted with caution.

4.6. *General conclusions*

While the ubiquitous dorsal/ventral dissociation between familiarity and recollection was found using both the remember/know test and the source memory procedure, further distinctions were found within the left PPC when these two methods were directly compared. In the dorsal PPC regions, where activity is most likely reflecting a cognitive process related to memory retrieval, there was a significant difference in the magnitude of familiarity-related activity between the two tests. This difference is most likely explained in terms of differences in task demands such as top-down attention or retrieval orienting, between the source and remember/know tests. In the ventral PPC regions, where there is less of a consensus in the literature, a difference not only in the magnitude of recollection-related activity but also in the extent of this activity was observed between the two tests. This modulation of activity within the ventral parietal regions could be explained either by the output buffer hypothesis or with the dual-attentional hypothesis. If we do not look at this study in isolation, but instead combine results from other experimental techniques (structural and functional connectivity studies, patient data, etc.) it seems more likely that this differential activity is representing some difference in cognitive demands (i.e. bottom-up attention or self-referential processing) between the tasks. Furthermore, if an episodic buffer theory is used to explain the differential ventral PPC activations, then one must assume that recollection is a graded, as opposed to a threshold (all-or-none) process, which is in debate in the literature (Mandler, 1980; Yonelinas, 1997 , 2001; but see Wixted, 2007; Mickes, Wais, & Wixted, 2009). For these reasons, we assume the most parsimonious explanation of the differential ventral PPC activation observed in the current study is a reflection of a difference in some cognitive process(es) associated with each task. Regardless of what theory is used to explain the differences observed, the fact that these differences exist between the tasks is enough to challenge the widely held belief that these two methods are functionally equivalent at separating the neural correlates of recollection and familiarity. With such a heated debate in the memory literature as to what functional role(s) (if any) the PPC is playing during memory retrieval, activation differences due simply to the procedure used to probe recollection and familiarity must be considered.

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Appendix. Remember/know Instructions

You will be presented with a series of words. Half of the words shown will be from the study list, the other half will be new words. By 'study list', I mean the four lists of words you initially saw, and made either an 'Abstract/Concrete' or 'Pleasant/Unpleasant' decision on.

For each word, please respond with either a "Remember", "Know", or "New" response. Each word will be on the screen for about 3 s.

A "Remember" response should be made when you recognize the word and can consciously recollect its prior occurrence in the study list. "Remember" is the ability to become consciously aware again of some aspect or aspects of what happened or what was experienced at the time the word was presented (e.g., aspects of the physical appearance of the word, or of something that happened in the room, or of what you were thinking and doing at the time). In other words, the "remembered" word should bring back to mind a particular association, image, or something more personal from the time of study, or something about its appearance or position (i.e., what came before or after that word). Please indicate a "remember" response by pressing button number 1—the button all the way to the left under your index finger.

A "Know" response should be made when you recognize the word from the study list, but you cannot consciously recollect anything about its actual occurrence or what happened or what was experienced at the time of its occurrence. In other words, respond with a "K" (for "know") when you are quite certain of recognizing the word, but the word fails to evoke a specific conscious recollection from the study list. Please indicate a "know" response by pressing button number 2—the button under your middle finger.

I want to emphasize that the difference between a "Remember" response and a "Know" response is NOT merely a difference in confidence. In both cases, you are quite certain that the word was on the study list. The different responses reflect a different kind of memory EXPERIENCE. A "Remember" response should bring you back to the time you encountered the word during the study session—almost as if you are re-experiencing that event. A "Know" response does not have this kind of experience, but instead reflects a sense of familiarity in the absence of contextual details.

A "New" response means that you do not think that the word was on the study list. You have no awareness of the word being shown previously. Please indicate this response by pressing button number 3 with your ring finger.

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