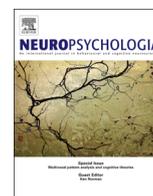




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Lateral posterior parietal activity during source memory judgments of perceived and imagined events



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ABSTRACT

Memories of real and imagined events are qualitatively distinct, and therefore may be supported by different neural mechanisms. In the present study, we tested whether brain regions are differentially activated during source discriminations of perceived versus imagined events. During the encoding phase, subjects perceived and imagined images of objects in response to a cue word. Then, at test, they made judgments about whether old and new cue words corresponded to items that were previously perceived or imagined, or if they were new. The results demonstrated that the left lateral posterior parietal cortex and dorsolateral prefrontal cortex were significantly more active during source attributions of perceived compared to imagined events. In addition, activity in these regions was associated with successful item memory (hits > correct rejections) for perceived, but not imagined events. These findings of a source-based dissociation of successful retrieval activity have important implications regarding theories of parietal contributions to recognition memory.

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1. Introduction

Fundamental to source monitoring theory is the notion that memories of events are comprised of different features, including perceptual, spatial, and temporal details, affective information, and information about the cognitive operations engaged during encoding (Johnson, Hashtroudi, & Lindsay, 1993). It is these contextual details that collectively provide cues that allow us to make decisions about item history (whether information is old or new), as well as the source or origin of memory representations (Johnson, 1997; Johnson & Raye, 1981, 2000; Johnson et al., 1993). Contextual memory models (e.g., Johnson et al., 1993; Schacter, Norman, & Koutstaal, 1998) distinguish between contextual details that were derived through perception (e.g., spatial layout, shape, size, color of objects) and those that were generated internally (e.g., thoughts, feelings). Several brain regions, including regions of the lateral posterior parietal cortex (PPC), appear to be associated with the retrieval of these contextual details (Vilberg & Rugg, 2007; Wheeler & Buckner, 2003; Yonelinas, Otten, Shaw, & Rugg, 2005). However, it is unclear whether these regions are sensitive to the internal/external source detail distinction, or whether they play a more general role in supporting the retrieval of contextual details of memories, regardless of source. The goal of the present experiment was to examine whether there are brain regions that

respond more during retrieval of memories of perceptually derived events compared to internally generated events.

Memories from perception and imagination have been shown to differ with respect to the relative amount of different types of qualitative features they contain. Memories of real events tend to contain more perceptually based contextual details than memories of internally generated events (Hashtroudi, Johnson, & Chrosniak, 1990; Johnson, Foley, Suengas, & Raye, 1988; Johnson, Raye, Foley, & Kim, 1982; Johnson, Raye, Foley, & Foley, 1981; Lampinen, Odegard, & Bullington, 2003; Schooler, Gerhard, & Loftus, 1986; Suengas & Johnson, 1988), which instead contain more reflective details, or information regarding the cognitive operations that were engaged during encoding (Johnson et al., 1981, 1988). Reality monitoring, which is a specific form of source monitoring that involves discriminating between the internal/external source of a memory, is thought to be based on a qualitative assessment of the features of memories from perception and imagination (see Johnson et al., 1993; Johnson & Raye, 2000 for reviews). According to source monitoring theory, when a memory is retrieved, it is assessed for the relative amount of these different qualitative details it contains, and then attributed to the source class it most closely resembles (Johnson et al., 1988, 1993).

Given that memories from perception and imagination are qualitatively distinct, and that reality monitoring discriminations are based on these differences, it is plausible that different neural substrates support the representation of these different kinds of contextual details during memory retrieval. Evidence in support of this notion comes from studies demonstrating that regions in the

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medial anterior PFC are more active when attention is focused on the contextual details of episodic memories that were internally generated as opposed to externally derived at encoding. Several studies have demonstrated that medial anterior PFC is more active when subjects make judgments about the task they performed during encoding compared to the spatial location (Simons, Owen, Fletcher, & Burgess, 2005a, temporal order (Simons, Owen, Fletcher, & Burgess, 2005b), or relative size (Dobbins & Wagner, 2005) of encoded stimuli. Other studies examined whether the medial anterior PFC responds more during retrieval of imagined compared to perceived events. While some studies found evidence for this source effect in medial anterior PFC (Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vinogradov et al., 2006) others did not (Lundstrom et al., 2003; Takahashi, Ohki, & Migashita, 2002). Thus, it appears that the anterior medial PFC is more active when attention is focused on the internally generated versus externally derived contextual details of episodic memories. However, it is unclear whether this region is more involved in the control mechanisms involved in directing attention toward these details, or the actual mnemonic representation of these reflective features.

Less work has been devoted to understanding whether there are brain regions that demonstrate the opposite pattern of response as the anterior PFC, responding more during retrieval of perceptually derived compared to internally generated contextual details of memories. Of the studies that compared brain activity during retrieval of internally/externally generated events, the opposite contrast revealing regions that were more active during retrieval of perceived compared to imagined events, regardless of response, was either not reported (Lundstrom et al., 2003; Vinogradov et al., 2006; Takahashi et al., 2002), or did not reveal any regions exhibiting differential activity (Turner et al., 2008). However, in these studies, because the goal was to identify regions that respond more during retrieval of internally generated information, the design was not optimized for observing regions responsive to externally derived mnemonic details. Memories for perceptually derived experiences are distinguishable from memories of internally generated events because they contain greater sensory information. However, in these studies, the presented stimuli were not perceptually rich, which may explain the failure to detect any regions that consistently responded more during retrieval of externally derived compared to internally generated mnemonic information. Perhaps relying on a task that involves the encoding of more perceptually rich visual stimuli might reveal a region or network of regions that respond in this manner.

Other studies have used similar paradigms in order to examine brain activity associated with a particular type of reality monitoring error that occurs when memories of internally generated events are mistakenly thought to reflect reality (false memories). In these studies, subjects perceived and imagined images in response to a cue and then after a delay made internal/external source monitoring judgments (Gonsalves & Paller, 2000; Gonsalves, Reber, Gitelman, Parrish, Mesulam, & Paller, 2004; Kensinger & Schacter, 2006; Okado & Stark, 2003; Simons, Henson, Gilbert, & Fletcher, 2008a; Takahashi et al., 2002). The results revealed that patterns of brain activity associated with both encoding and retrieval of internally generated events differ depending upon whether memories for these events are accurately attributed to internal thought processes or mistakenly thought to be the result of a perceptually experienced event. These findings provide insight regarding the neural processes that lead to accurate versus inaccurate reality monitoring discriminations. However, they do not directly address differences in the neural mechanisms involved in the mnemonic representation of internally generated versus externally derived events, regardless of the accuracy of the response, which was the goal of the present study.

One potential region that might exhibit greater activity during retrieval of externally derived compared to internally generated events is the lateral posterior parietal cortex (PPC). This region has recently received ample attention from memory researchers due to the consistent finding that regions of the lateral PPC are significantly more active during correct recognition of studied items compared to correct rejection of new items (e.g. Kahn, Davachi, & Wagner, 2004; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). This effect, which has been referred to as the parietal old/new effect or the parietal successful retrieval effect, has been observed across a wide range of experimental stimuli and response contingencies (see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Levy, 2012; Vilberg & Rugg, 2008; Wagner et al., 2005 for reviews). Regions of the lateral PPC are also commonly found to be more active during source memory compared to item memory judgments (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Wagner, 2005; Fan, Snodgrass, & Bilder, 2003; Han, O'Connor, Eslick, & Dobbins, 2012). Because source memory involves the retrieval of greater contextual details than item memory alone, these studies suggest that lateral PPC may contribute to the retrieval of contextual details that are associated with episodic memories. However, it is unclear whether the lateral PPC contributes generally to the mnemonic representation of contextual details, or like the PFC, it plays a more specific role in representing only a subset of these details. The majority of the fMRI studies examining parietal successful retrieval activity have relied on paradigms that involve the external presentation of visual, and occasionally auditory stimuli. Far fewer have investigated memory for internally generated events, and to our knowledge no studies have systematically investigated whether the magnitude of parietal recognition activity varies according to internal/external source. Thus, the lateral PPC may play a prominent role in the retrieval of memories of real versus internally generated events. In support of this notion, although lateral parietal patients do not typically exhibit recognition memory deficiencies, they do tend to report a lack of richness or vividness as well as a lack of confidence in their memories (Ally, Simons, McKeever, Peers, & Budson, 2008; Davidson et al., 2008; Haramati, Soroker, Dudai, & Levy, 2008; Simons et al., 2008b). This suggests that lateral parietal patients may have a deficit in representing the perceptually based contextual details that typically pertain more to memories of real than imagined events.

Evidence that lateral PPC responds more during retrieval of externally derived compared to internally generated memories would provide insight regarding the role of this region in recognition memory. Despite the consistency of observed effects in lateral PPC during recognition memory, the precise functional role of this region remains uncertain. Several hypotheses have been proposed to account for these effects (e.g. Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008; Donaldson, Wheeler, & Peterson, 2010; Shimamura, 2011; Vilberg & Rugg, 2008; Wagner et al., 2005). However, fundamental to understanding the contributions of the lateral PPC to recognition memory is deciphering whether this region contributes to processes necessary for successful retrieval; processes such as directing attention or monitoring retrieved information, or whether it plays a role in the actual representation or maintenance of stored information. The present study will provide insight regarding theories of parietal contributions to recognition memory by examining whether parietal activity varies according to internal/external source and source attribution.

In order to examine whether recognition activity in the lateral PPC varies as a function of internal/external source and source attribution, we measured brain activity during a two-part reality monitoring experiment. In the first phase, subjects perceived and imagined images of objects in response to a cue word. Then, at test, they saw old and new cue words and decided whether each

word corresponded to an item that was previously perceived or imagined, or if the word was new. We then analyzed brain activity according to both trial type and response. We expected that lateral PPC would be more active during retrieval of previously perceived compared to imagined events, which would suggest that lateral PPC plays a preferential role in representing externally derived mnemonic information.

2. Material and methods

2.1. Participants

Twenty subjects (11 females, 9 males; ages 20–51, $M=28.1$) from the University of California, Santa Barbara community volunteered to participate in response to an e-mail distributed to graduate students and staff. All subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Two additional subjects participated but were excluded from analysis. One subject was excluded due to a technical error in data acquisition, while the other was excluded due to her inability to complete the experiment. All subjects gave informed consent according to the procedures approved by the UCSB Institutional Review Board and were paid \$100 for their participation.

2.2. Stimuli and apparatus

Stimuli consisted of 750 photographs of objects on a white background and 750 corresponding words. Photos were centered on the screen and average dimensions were 132×257 pixels (x range: 69–1520; y range: 59–1159). Words corresponding to the photos were 2–25 characters long ($M=8.5$), and in most instances were a single word, however in some cases were two to three words (e.g., “alarm clock,” “orange juice carton”). Words were centered on the screen and were presented in 48-point Helvetica font. Stimuli were presented with the MATLAB Psychophysics Toolbox (www.psychtoolbox.org) on a MacBook Pro, which was synchronized with the onset of each functional scan in order to assure accuracy of event timing. All images were projected onto a screen situated at the head of the scanner, made visible to the participants by a mirror mounted to the head coil. Behavioral responses and reaction times were obtained by a fiber optic button box inside the scanner, and responses were recorded in MATLAB.

2.3. Design and procedure

Subjects were scanned during two sessions, separated by 24 h. The encoding phase took place on the first day of the experiment. Subjects were told they were participating in a visual imagery experiment, and were not informed about the memory component of the experiment in order to lessen the likelihood that they would adopt an alternative mnemonic encoding strategy (e.g., rehearsal) instead of trying to visualize imagine trials. They were told that the second day of testing

would be very similar to the first day, and that the reason we needed them to return for additional testing was that we required a large number of trials for signal averaging. Subjects were not asked about whether they suspected there would be a subsequent memory test; however, in general, they appeared surprised when they were informed of the memory component of the experiment upon arrival for the second day of testing.

There were two types of trials in the encoding phase. All trials began with the presentation of a word that named a common object. For *perceive trials* (Fig. 1a), a photo corresponding to the word followed the presentation of the word. For *imagine trials* (Fig. 1b), a black rectangle, serving as a cue for subjects to visually imagine the object, followed the presentation of the word. In both conditions, stimuli were presented for one second each, intermixed with two, one-second central fixation crosses, resulting in four-second trials. On all trials, subjects were instructed to respond by pressing a button in the last two seconds of the trial, following the presentation of the photo or rectangle, indicating whether they judged each item to be bigger than, smaller than, or about the same size of a shoebox. Each of the 10 functional runs consisted of 25 perceive and 25 imagine trials that were randomly intermixed.

To introduce jitter for purposes of statistical modeling, 4 s fixation trials were intermixed with perceive and imagine trials. The optimal sequence for the order of presentation of trials by condition was determined by randomly generating a series of event sequences ($n=1000$) with the specified parameters (number of events, number of trials per event, trial length), creating design matrices from these sequences, and then finding the design matrix with the smallest maximum eigenvalue of the inverse information matrix. The same sequence was used for all subjects, however for each subject, the order for which stimuli appeared and the conditions they were assigned to were randomly determined.

Subjects returned 24 h following the onset of the first phase of the experiment for the test session (Fig. 1c). On each trial, a word was presented for 2 s, and subjects indicated via button press whether they believed the word corresponded to an object that was initially perceived or imagined, or if the word was new. All subjects were instructed to indicate a “new” response by pressing a button with their left hand index finger. Half of the subjects were instructed to use their right-hand index finger to indicate a “perceived” response, and their right-hand middle finger to indicate an “imagined” response. For the other half of the subjects, the right-hand responses were reversed. In each of the 10 functional runs, 25 perceive, 25 imagine, and 25 new words were presented according to the same optimal design procedure used in the first session, with adjusted parameters. For behavioral

Table 1

Abbreviations and mean (standard deviation) proportion of trials within each trial type – response condition.

Response	Trial type		
	Photo	Imagine	New
Perceived	PP=0.48 (0.18)	IP=0.21 (0.17)	NP=0.12 (0.11)
Imagined	PI=0.36 (0.13)	II=0.60 (0.20)	NI=0.30 (0.18)
New	PN=0.15 (0.10)	IN=0.19 (0.12)	NN=0.58 (0.18)

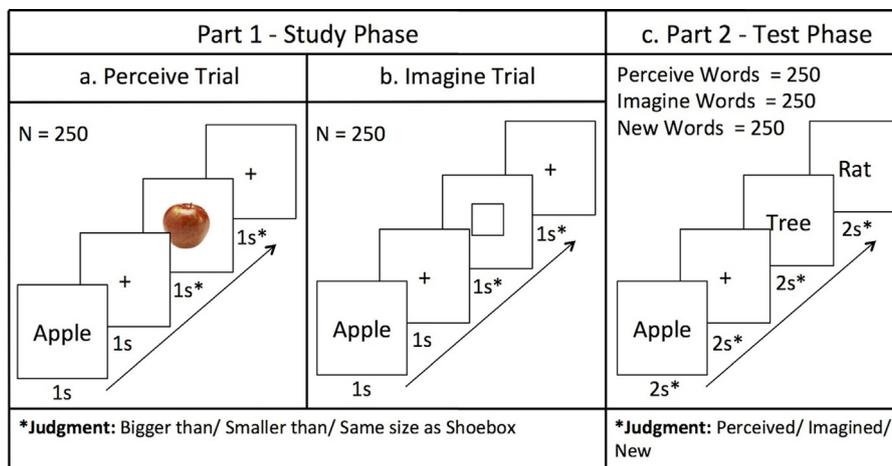


Fig. 1. Schematic representation of experimental task and design. The study session included both perceive trials (a) and imagine trials (b). All trials began with the presentation of a cue word, which was a name of a common object, presented for 1 s, followed by the presentation of a central fixation cross for 1 s. On *perceive trials*, a photo of an object corresponding to the cue word was presented for 1 s following the cue word, which indicated to subjects that they should try to visually imagine what the object looked like. All trials ended with a 1 s fixation cross. On all trials, the task was to decide and indicate via button press whether the object (in real life) was bigger than, smaller than, or about the same size as a shoebox. Subjects were instructed to respond during the last 2 s of the trial. During the test phase (c), all of the cue words from the encoding phase, along with 250 new words were presented for 2 s each. Subjects decided and indicated via button press whether each word corresponded to an image that was previously perceived or imagined, or if it was new.

and functional analyses, each event was classified according to trial type (perceive, imagine, new) and response (perceived, imagined, new). We will refer to the conditions of interest by their trial type–response condition abbreviations (see Table 1), with the first letter in the abbreviation referring to the source (P=Perceive, I=Imagine, N=New) and the second letter referring to the response (P=Perceived, I=Imagined, N=New). The nine trial type–response conditions include: perceive trials, perceived response (PP); perceive trials, imagined response (PI); perceive trials, new response (PN); imagine trials, perceived response (IP); imagine trials, imagined response (II); imagine trials, new response (IN); new trials, perceived response (NP); new trials, imagined response (NI); and new trials, new response (NN, also referred to as correct rejection).

2.4. fMRI acquisition

Imaging was performed at the UCSB Brain Imaging Center on a 3T Siemens TIM Trio scanner with a standard 12-channel coil. Subjects were scanned during both encoding and retrieval phases. Each scanning session included 10 functional runs comprised of a series of T2*-weighted whole-brain echoplanar images (EPI) (2000 ms repetition time (TR), 30 ms echo time (TE), 90° flip angle). Each volume consisted of 37 slices acquired parallel to the AC-PC line (interleaved acquisition; 3 mm slice thickness, 64 × 64 matrix). Four volumes were discarded prior to the onset of each run in order to allow for tissue magnetization, followed by a series of volumes ranging from 210 to 250 ($M=226.8$) in the first session, and 152–173 ($M=161.6$) volumes in the second session. The number of volumes varied across experimental runs because the algorithm used to produce an optimal sequence created vectors that varied in length. However, the number of volumes per run was consistent across all subjects. At the start of the second day, an anatomical scan was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; TR=2300 ms; TE=2.98 ms; FA=9°; 160 sagittal slices; 1.1 mm thick; 256 × 256 matrix). Scanning sessions lasted roughly one hour and 45 min each day.

2.5. Pre-processing

Standard preprocessing was conducted using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). For each subject, time-series data were realigned to the mean functional image and sampled according to a 7th degree B-spline interpolation method. Motion parameters were examined for each subject and runs that included movements greater than 3 mm in any direction were excluded from analysis (a single run for a single subject was excluded). Co-registration was performed as a three-step process, using a normalized mutual information cost function and 12-parameter affine transformations. First, the mean functional image was co-registered to the anatomical image. Next, the anatomical image was normalized to the SPM5 template image (MNI Avg152, T1 2 × 2 × 2 mm) and re-sampled with 2nd degree B-spline interpolation. Finally, the parameters from this transformation were used to register the functional images into MNI stereotaxic space. After normalization, data were spatially smoothed using an 8 mm full-width-half-maximum Gaussian kernel in order to reduce noise.

2.6. Statistical modeling

Event-related data from the encoding and retrieval phases were modeled and estimated separately using the general linear model (GLM) for each individual subject. The hemodynamic response was estimated for six event types of interest (PP, PI, PN, IP, II, IN) for encoding phase data, and nine event types of interest for retrieval phase data (PP, PI, PN, IP, II, IN, NP, NI, NN), with one additional event in both encoding and retrieval phases for trials that involved no response or multiple responses. Estimation was based on the SPM5 canonical HRF model without derivatives. Autoregressive AR(1) models used globally over the whole brain were applied during parameter estimation in order to correct for time-series correlations in the data. Contrasts were constructed for each of the six encoding events of interest and each of the nine retrieval events of interest compared to baseline. The resulting contrast images were then entered into two separate second-level, random effects, repeated measures factorial models, treating subjects as the random variable (encoding phase: 2 × 3: source (perceive, imagine) × subsequent response (perceived, imagined, new); retrieval phase: 3 × 3: source (perceive, imagine, new) × response (perceived, imagined, new)). To account for within-subjects correlation of measures due to the repeated measures design, the covariance components were estimated with Restricted Maximum Likelihood (ReML) in SPM5 and used to adjust the statistics and degrees of freedom during inference.

2.7. Regions of interest analysis

Because we were particularly interested in how activity would vary as a function of source and source attribution in lateral parietal regions that typically exhibit successful retrieval effects, we ran several regions of interest (ROI) analyses

to more closely examine how activity varies as a function of source, response, and accuracy in these regions. Eight regions, which included left and right superior parietal lobe (SPL), inferior parietal lobe (IPL), angular (ANG) and supramarginal (SMG) gyri were defined according to the Automated Anatomical Labeling (AAL) ROI library (Tzourio-Mazoyer et al., 2002). Two additional regions were functionally defined from the contrast of all old trials given an old response (PP, PI, IP, II) compared to correct rejections (NN). The first region included all voxels within the largest cluster of activation in the parietal cortex, whereas the second region was a 6 mm sphere centered around the peak of activity in the parietal cortex. For each of the six regions of interest, the average blood–oxygen level-dependent (BOLD) percent signal change was estimated using the MarsBar toolbox in SPM5 (Brett, Anton, Valabregue, & Poline, 2002) for each of the nine conditions of interest (PP, PI, PN, IP, II, IN, NP, NI, NN).

3. Results

3.1. Behavioral results

Reaction times were assessed and compared across perceived/imagined conditions for both the encoding and retrieval phases (Table 2). There were no significant differences in reaction time according to source during the encoding or retrieval phases ($p > 0.05$). Memory performance for perceived and imagined events was evaluated in terms of both item and source memory. Item memory was assessed according to a traditional Signal Detection Theory (SDT) approach (Green & Swets, 1966) and sensitivity (d') was calculated for each subject. Both “perceived” and “imagined” responses were collectively considered “old” responses, and therefore hits included both accurately attributed as well as misattributed items. Source monitoring performance was assessed using the conditional source identification measure (CSIM; Murnane & Bayen, 1996). In addition, the behavioral data were analyzed using a multinomial processing model (MPM) for three sources, which provides probability estimates for item memory (detectability (D) – probability of detecting an item as old), source memory (discriminability (d) – probability of correctly attributing the source of detected items), and several forms of guessing biases via maximum-likelihood parameter estimation (Riefer, Hu, & Batchelder, 1994; Batchelder & Riefer, 1990). These behavioral measures are presented in Table 2. Item memory as assessed by SDT was better for perceived compared to imagined events ($t(38)=3.305$, $p < 0.01$). However, of the items recognized as old source identification (CSIM) was better for imagine trials compared to perceive trials ($t(38)=2.473$, $p < 0.05$). From the MPM estimation, the parameter g , which reflects the probability of guessing “perceived” to a non-detected item was estimated to

Table 2

Mean and (standard error) reaction time (RT) and behavioral performance for perceived and imagined events.

Behavioral measure	Source	
	Perceived	Imagined
Encoding RT	0.89 (0.03)	0.87 (0.03)
Retrieval RT	1.34 (0.02)	1.35 (0.02)
Item memory		
SDT (d')	1.35 (0.11)	1.21 (0.11)
MPM (D)	0.74 (0.04)	0.68 (0.05)
Source memory		
CSIM	0.56 (0.18)	0.74 (0.05)
MPM (d)	0.47 (0.07)	0.13 (0.21)

Note—SDT=Signal Detection theory; MPM=multinomial processing model; (d')=sensitivity; (D)=detectability; CSIM=conditional source identification measure; (d)=discriminability.

be 0.29 (95% confidence interval: 0.20–0.38), which demonstrates subjects' bias to respond "imagined" to undetected items.

3.2. fMRI whole-brain results

Encoding and retrieval data were analyzed separately according to two random effects, full-factorial designs. In order to reduce the likelihood of Type I error, only clusters of at least 10 contiguous voxels that survived the false discovery rate (FDR) correction ($\alpha=0.05$) were considered. To locate anatomical regions, MNI coordinates were transformed into Talairach space with the MatLab function `mni2tal` (<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>) and entered into Talairach Client software (Lancaster et al., 1997; Lancaster et al., 2000). All coordinates are reported in MNI $\{x, y, z\}$ stereotaxic space.

3.2.1. Encoding

Although our main focus was on retrieval related activity, we also examined the encoding data in order to assess overall differences in brain activity according to source. We inclusively masked the perceived (PP+PI+PN) > baseline contrast with the imagined (IP+II+IN) > baseline contrast (uncorrected mask $p\text{-value}=p < 0.001$) in order to determine which regions were active in both encoding conditions (Fig. 2, Table 3). Overall, brain activity associated with encoding of perceived and imagined events was highly overlapping. Regions that were active for both the perceived > baseline as well as imagined > baseline contrasts included much of the posterior parietal cortex and prefrontal cortex bilaterally, along with the insula, and visual processing regions in the occipital and temporal lobes. We also looked at main effects of source to see whether there were brain regions that were significantly more active during the perceive or imagine conditions. Consistent with previous research (e.g. Ganis, Thompson, & Kosslyn, 2006; Kosslyn, Thompson, & Alpert, 1997; Stokes, Thompson, Cusack, & Duncan, 2009), perceived events were associated with greater activity than imagined events in posterior visual processing regions, including much of the occipital lobe, as well as the more ventral aspects of the temporal cortex and the most dorsal aspects of the parietal lobe. Imagined events were associated with greater activity than perceived events in mostly prefrontal regions, but also in more dorsal temporal and ventral parietal regions.

3.2.2. Retrieval

To analyze whole-brain effects at retrieval, we first examined whether there were overall differences in brain activity according to source and source attribution. We then compared whole-brain differences in activity for accurately attributed items compared to misattributed items (PP+II > PI+IP). Finally, because we were interested in how regions involved in successful retrieval vary according to internal/external source and source attribution, we compared activity associated with each of the conditions that involved an old ("perceived" or "imagined") response to a studied item (PP, PI, IP, and II trials) to activity associated with correct rejection (NN) trials. Brain activity during false alarm trials, which included both NP and NI trials, was also compared to activity during correct rejections (NN).

3.2.2.1. Main effect of source. At test, regardless of source attribution, items that were initially perceived (PP+PI+PN) elicited greater activity than items that were initially imagined (IP+II+IN) in several left-hemisphere regions (Fig. 3a, Table 4). A large cluster of activation was centered on the left angular gyrus (BA39) and extended to the cuneus, precuneus, IPL, SPL, middle occipital gyrus, and middle temporal gyrus (BAs: 7, 19, 39, 40).

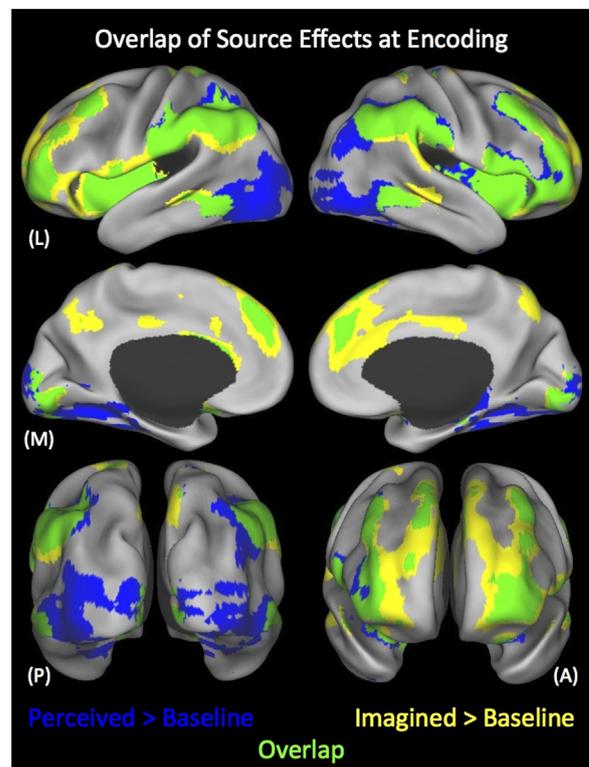


Fig. 2. Independent and overlapping effects of perceived trials and imagined trials compared to baseline at encoding. Regions shown in blue were active in the perceive > baseline contrast and not the imagine > baseline contrast; regions in yellow were active in the imagine > baseline contrast and not the perceive > baseline contrast; regions in green were active in both perceive > baseline and imagine > baseline contrasts. Contrasts were thresholded at an uncorrected $p < 0.001$ threshold. Activations are displayed on the inflated surface caret brains (Caret5) in (L) lateral, (M) medial, (P) posterior, and (A) anterior views (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Other activations included a region in the cuneus/precuneus (BAs: 7, 18, 19), as well as a cluster centered on the left precentral gyrus (BA6) with activity extending to the postcentral gyrus, and the inferior and middle frontal gyri (BAs: 2, 3, 6, 9, 40, 46). Smaller left hemisphere clusters were centered on the left fusiform gyrus (BA37), the left insula (BA13), and the left cingulate gyrus (BA23). The only right hemisphere activations included clusters in the right cerebellum, the right caudate, and the right middle frontal gyrus (BA9/46).

In contrast to the left-hemisphere regions elicited by the perceive > imagine contrast, the comparison of test phase activity associated with items that were initially imagined (IP+II+IN) compared to perceived (PP+PI+PN), regardless of response resulted in extensive right hemisphere activations (Fig. 3a, Table 4). However, an examination of the beta values in each of these right hemisphere cortical regions revealed that this main effect was driven by a deactivation below baseline during retrieval of perceived events that was not evident during retrieval of imagined events. The largest cluster revealed from the imagined > perceived contrast was in the postcentral gyrus (BA3), and significant voxels within the cluster extended to the precentral gyrus, precuneus, SPL, and SMG (BAs: 1, 4, 5, 6, 7, 40). Smaller clusters in the right hemisphere were centered in the superior frontal gyrus (BA9), the superior temporal gyrus (BA13), the middle temporal gyrus (BA37), the cingulate gyrus (BA31) and the putamen. There were a few small left hemisphere regions that exhibited significantly different activity as well. One cluster was centered on the left medial anterior PFC (BA10) and extended into the right medial anterior PFC. Other left hemisphere regions included

Table 3
Whole brain encoding effects of perceived/imagined source

Anatomical region of center of mass	BA	x	y	z	t-Value	Cluster volume
Regions active in both perceived (PP+PI+PN) and imagined (IP+II+IN) conditions						
L superior parietal lobe	7	−42	−63	51	7.12	553
R inferior parietal lobe	40	51	−48	57	7.60	412
L postcentral gyrus	7	−12	−60	72	3.82	21
R superior parietal lobe	7	9	−75	60	5.23	17
R inferior parietal lobe	14	33	−51	36	3.31	14
L inferior frontal gyrus	10	−42	54	6	5.95	559
L superior frontal gyrus	6	−12	27	63	3.63	16
R superior frontal gyrus	6	15	27	63	4.33	34
L medial frontal gyrus	9	−9	39	33	3.13	47
R medial frontal gyrus	9	9	39	36	2.89	22
R fusiform gyrus	37	48	−63	−21	11.68	1378
R middle temporal gyrus	37	57	−54	−9	7.76	48
L middle occipital gyrus	37	−54	−63	−15	7.11	10
L insula	13	−42	−3	12	8.45	2746
L/R thalamus	−	0	−9	9	3.04	11
R caudate	−	30	−36	6	5.60	120
L cerebellum	−	−39	−57	−39	4.84	27
R cerebellum	−	33	−39	−33	4.45	118
Perceived (PP+PI+PN) > imagined (IP+II+IN)						
L superior parietal lobe	7	−27	−72	51	3.04	23
R postcentral gyrus	1	63	−27	45	4.04	25
R middle frontal gyrus	46	51	36	15	7.15	345
R fusiform gyrus	37	42	−60	−12	17.66	2405
R middle temporal gyrus	21	36	−3	−33	4.19	10
L amygdala	−	−27	0	−21	4.35	22
R amygdala	−	21	−3	−12	3.48	23
L cerebellum	−	−30	−63	−12	17.81	2066
Imagined (IP+II+IN) > perceived (PP+PI+PN)						
L supramarginal gyrus	40	−60	−51	36	3.26	28
L supramarginal gyrus	40	−63	−51	24	3.74	52
L postcentral gyrus	3	−30	−27	45	3.17	17
L/R medial frontal gyrus	6	0	−12	75	4.13	39
R superior temporal gyrus	22	57	15	0	4.33	140
R middle temporal gyrus	21	54	−12	−24	3.81	18
L caudate	−	−21	−42	15	6.46	6765
L cerebellum	−	−3	−63	−12	5.51	647
R cerebellum	−	36	−57	−36	5.08	102
L cerebellum	−	−24	−87	−33	3.82	10
R cerebellum	−	12	−36	−42	3.80	25
L cerebellum	−	−42	−54	−39	3.49	12

Notes—x, y, z coordinates are in MNI space. Cluster volume is in cubic voxels. Regions commonly active during both perceived and imagined conditions were determined by inclusively masking the perceived > baseline (PP+PI+PN > baseline) {T} contrast with the imagined > baseline (IP+II+IN > baseline) {T} contrast ($p < 0.001$). Clusters revealed from the main effect of source contrasts are those that survived the FDR-corrected ($p < 0.05$) threshold. BA=brodmann area; L=left; R=right; PP=perceived trial, perceived response; PI=perceived trial, imagined response; PN=perceived trial, new response; IP=imagined trial, perceived response; II=imagined trial, imagined response; IN=imagined trial, new response; NP=new trial, perceived response; NI=new trial, imagined response, NN=new trial, new response.

two clusters in the cerebellum, a region in the middle temporal gyrus (BA2/37), the superior temporal gyrus (BA22). Overall, these results demonstrate that brain activity was greater during reality monitoring discriminations of perceived compared to imagined items in mostly left hemisphere regions, predominately in dorsolateral prefrontal and parietal cortex. In contrast, source discrimination of imagined items was associated with greater activity than source discrimination of perceived items mostly in the right hemisphere, again in frontal and parietal regions.

In source memory studies that involve the discrimination between two sources of information, the encoding and retrieval tasks interact, such that the correct response to an item encoded through Source A is not the same as the correct response to items that were encoded through Source B. In many source memory experiments, drawing inferences about activity associated with one specific source versus the other is not critical, and therefore these confounds can be combated by simply collapsing across source conditions. However, for our purposes

it was necessary that these conditions be kept separate. In order to be confident that source-based effects were actually due to encoding source, and not source attribution or accuracy, we examined source effects while controlling for accuracy and response in a number of different ways. The results of these comparisons are presented in Fig. 3. These comparisons revealed that source effects in left lateral PPC were evident when the analysis involved collapsing across all responses (PP+PI+PN > IS+II+IN; Fig. 3a), collapsing across all “old” responses (PP+PI > IP+II; Fig. 3b), when only trials given a “perceived” response were considered (PP > IP; Fig. 3c), when only trials given an “imagined” response were considered (PI > II; Fig. 3d), when only correct source attributions were considered (PP > II; Fig. 3e), and when only source misattributions were included in the analysis (PI > IP). Given that source effects were observed regardless of how response and accuracy were controlled for, we are confident that these source-based differences in activity were a result of the encoding source.

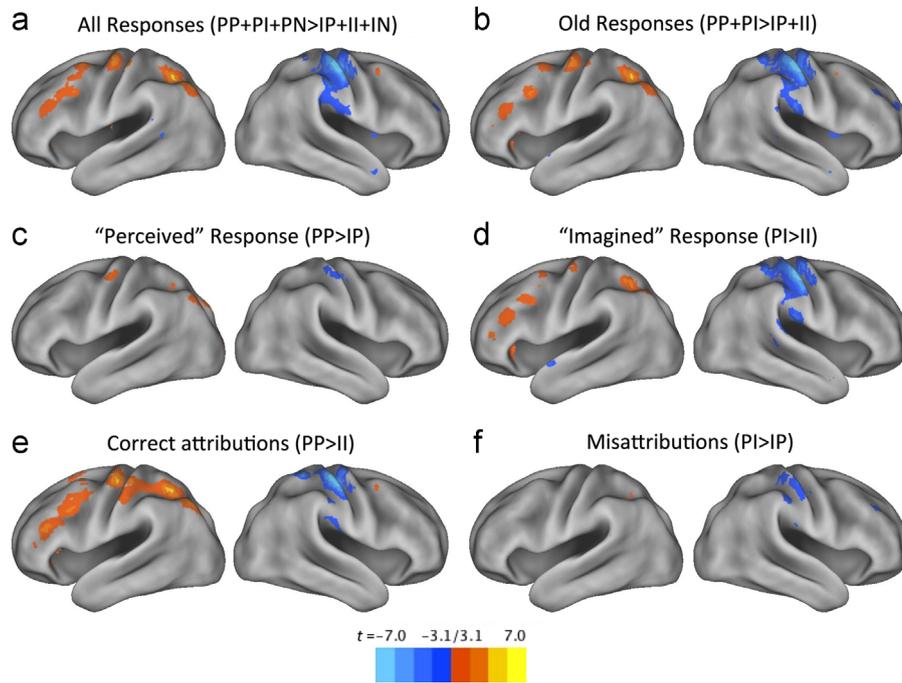


Fig. 3. Whole-brain, group-level main effects of source. Only cortical regions that survived the uncorrected $p < 0.001$ threshold are displayed. Activation clusters were mapped onto the inflated surface caret brain (Caret5) and presented from the lateral view. Source effects are displayed for (a) all responses ($PP+PI+PN > IP+II+IN$); (b) old responses only (“perceived” or “imagined” response) ($PP+PI > IP+II$); (c) trials that were given a “perceived” response ($PP > IP$); (d) trials that were given an “imagined” response ($PI > II$); (e) correct attributions only ($PP > II$); and (f) misattributions only ($PI > IP$). PP=perceive trial, perceived response; PI=perceive trial, imagined response; PN=perceive trial, new response, IP=imagine trial, perceived response; II=imagine trial, new response.

3.2.2.2. Main effect of source attribution. In order to examine whether brain activity varied as a function of source attribution, or the subjective feeling that memories resulted from either imagination or perception, we compared activity during retrieval of memories given a “perceived” ($PP+IP+NP$) versus an “imagined” ($PI+II+NI$) response. There were no significant differences in activity according to source attribution across the whole-brain at the group-level at the FDR-corrected threshold of $p < 0.05$.

3.2.2.3. Effect of source accuracy. To examine whether brain activity varied according to source accuracy during reality monitoring, we compared activity during accurately attributed items to activity associated with misattributions, both collapsing across source conditions ($PP+II > PI+IP$), as well as individually for each source condition (perceive trials: $PP > PI$, and imagine trials: $II > IP$). When collapsing across source conditions, the results revealed that one region, the right putamen, was more active during correct source attributions ($PP+II$) than misattributions ($PI+IP$). The opposite comparison of brain activity associated with misattributions versus correct attributions ($PI+IP > PP+II$) did not reveal any significant differences in activity. When tested individually, there were no effects of source accuracy for perceived trials ($PP > PI$) or imagined trials ($II > IP$).

3.2.2.4. Successful retrieval effects. In order to investigate how activity varies according to the perceived/imagined source of memories in regions that typically exhibit successful retrieval effects, we compared brain activity for each of the four conditions that involved an old response (“perceived” or “imagined”) to an old item (PP, PI, IP, II) to brain activity during correct rejections (NN; Fig. 4, Table 5). In addition, to analyze whether these successful retrieval effects were driven by item history (whether the item was presented at study or not) or

subjective response, we also compared brain activity during false alarm trials (old response to new item: $NP+NI$) to activity during correct rejections (NN).

Correctly attributed perceived events (PP) were associated with robust, left-lateralized successful retrieval activity (Fig. 4a, Table 5). A large cluster was centered on the left middle frontal gyrus (BA10), with activity extending to the inferior and superior frontal gyri, the precentral, postcentral, and cingulate gyri, and the insula (BAs: 2, 3, 4, 6, 8, 9, 10, 43, 45, 46). A second large cluster of activity was in the left IPL (BA40) extending to the cuneus, precuneus, SPL, angular and supramarginal gyri (BAs: 7, 19, 39, 40). Other smaller clusters of significant activation in the left hemisphere were centered in cerebellum, inferior/middle temporal gyri (BA20/37), postcentral gyrus (BA3), lingual/inferior occipital gyri (BA17), posterior cingulate (BA29), putamen, and inferior/middle occipital gyri (BA18/19). There were a few right hemisphere regions that also exhibited greater activity during PP compared to NN trials. Right hemisphere regions included a cluster centered in the right middle frontal gyrus (BA8), and the right cingulate gyrus (BA24), and a large portion of the cerebellum. Voxels included in the large left parietal cluster also extended into the right hemisphere, including regions in the right cuneus, precuneus, SPL, IPL, and supramarginal and angular gyri (BAs: 7, 18, 19, 39, 40).

Successful retrieval activity associated with misattributed perceived events (PI) was similar to activity associated with correctly attributed perceived events (PP), only activity was not quite as significant or extensive (Fig. 4b, Table 5). Similarly to the $PP > NN$ contrast, the two largest clusters of active voxels revealed from the $PI > NN$ contrast were in the left middle frontal gyrus (BA10), extending to the inferior and superior frontal gyri, cingulate gyrus, and insula (BAs: 6, 8, 9, 10, 44, 45, 46, 47), and in the left IPL (BA40), extending to the SPL, precuneus, and angular and supramarginal gyri (BAs: 7, 19, 39, 40). Other left hemisphere regions included the thalamus/caudate, middle temporal gyrus, cingulate gyrus (BA32), precuneus (BA7/19), putamen, and cerebellum. Right

Table 4

Whole-brain main effects of source (perceived compared to imagined trials), source attribution (“perceived” compared to “imagined” response), and source accuracy (correct source vs. incorrect source).

Anatomical region of center of mass	BA	x	y	z	t-Value	Cluster volume
Perceived trials (PP+PI+PN) > imagined trials (IP+II+IN)						
L angular gyrus	39	-36	-57	45	5.44	363
L precentral gyrus	6	-36	6	36	4.92	422
R middle frontal gyrus	46	51	39	18	3.75	23
L superior frontal gyrus	6	-9	18	51	3.72	38
L cuneus	18	-9	-75	33	5.03	196
L fusiform gyrus	37	-30	-39	-15	4.41	16
L insula	13	-39	-21	21	4.26	14
L cingulate gyrus	23	-6	-24	27	4.08	13
R caudate	-	9	9	0	4.97	301
R cerebellum	-	12	-54	-15	5.40	63
Imagined trials (IP+II+IN) > perceived trials (PP+PI+PN)						
R postcentral gyrus	3	45	-21	57	6.98	980
R superior frontal gyrus	9	30	42	27	3.56	15
L medial frontal gyrus	10	-9	-45	15	3.84	22
L middle temporal gyrus	37	-57	-63	6	4.19	27
R superior temporal gyrus	13	45	3	-18	4.02	18
L superior temporal gyrus	22	-63	-42	24	3.90	28
R middle temporal gyrus	37	54	-66	3	3.86	14
R cingulate gyrus	31	15	-27	48	3.74	11
R putamen	-	30	-12	0	4.17	65
L cerebellum	-	-15	-54	-21	4.92	59
L cerebellum	-	-30	-45	-30	4.00	14
Perceived response (PP+IP+NP) > imagined response (PI+II+NI)						
No suprathreshold clusters.						
Imagined response (PI+II+NI) > perceived response (PP+IP+NP)						
No suprathreshold clusters.						
Source correct > source incorrect (PP+II > PI+IP)						
No suprathreshold clusters.						

Notes—x, y, and z coordinates are in MNI space. Cluster volume is in cubic voxels. Significant clusters are those that survived the FDR-corrected ($p < 0.05$) threshold. BA=Brodman area; L=left; R=right; PP=perceived trial, perceived response; PI=perceived trial, imagined response; PN=perceived trial, new response; IP=imagined trial, perceived response; II=imagined trial, imagined response; IN=imagined trial, new response; NP=new trial, perceived response; NI=new trial, imagined response, NN=new trial, new response.

hemisphere regions included the IPL (BA40, 39), the middle frontal gyrus (BA8), the superior frontal gyrus (BA 9/10), the thalamus and cerebellum.

In contrast to each of the perceive conditions, comparisons of activity associated with imagined trials versus correct rejections did not result in widespread left hemisphere activations. For the IP > NN comparison (Fig. 4d, Table 5), the only left hemisphere activations were in the prefrontal cortex, in the superior/middle frontal gyri (BA9/10, 46/47), the middle frontal gyrus (BA6), and the medial frontal gyrus (BA9). The largest right hemisphere cluster of activity was in the precentral/postcentral gyri (BA3/4). Other right hemisphere activations included the cingulate gyrus (BA32), the supramarginal gyrus (BA40), the middle frontal gyrus (BAs 8, 9, 10), and the superior frontal gyrus (BA6).

For accurately attributed imagined trials compared to correct rejections (II > NN), the largest cluster of voxels was again centered on the right precentral gyrus (BA4), extending to the IPL and postcentral gyrus (BAs: 2, 3, 40; Fig. 4e, Table 5). Other regions exhibiting greater activity for II compared to NN trials included the left inferior/middle frontal gyri (BA10/46), the left cingulate gyrus (BA31), and the left putamen. Finally, when false alarms, which

included both NP and NI trials were compared to correct rejections (NN), one cluster of voxels was revealed which was centered in the left middle frontal gyrus (Fig. 4f, Table 5).

The results of these analyses revealed that successful retrieval effects in the lateral parietal and dorsolateral PFC vary according to the internal/external source of encoded information. Successful retrieval effects were observed in the lateral PPC during recognition of perceived items, both when item recognition was and was not accompanied by source memory. However, for imagined items, there was hardly any evidence for successful retrieval activity in the lateral PPC.

3.3. Regions of interest (ROI) analysis

In order to further investigate how internal/external source and source attribution are associated with differences in activity in the parietal cortex, we estimated the average percent signal change (PSC) in 10 ROIs for each of the conditions of interest (PP, PI, PN, IP, II, IN, NP, NI, NN). These regions consisted of eight parietal regions anatomically defined by the AAL atlas in Marsbar (Tzourio-Mazoyer et al., 2002) including left and right SPL, IPL, angular gyrus, and supramarginal gyrus (Fig. 5a–h). In addition, activity within two functionally defined regions was analyzed (Fig. 5i and j). These regions were defined from the contrast of all old items called old vs. correct rejections (PP+PI+IP+II > NN). The first region included all voxels in the left lateral parietal cortex that survived the threshold criterion (cluster extent=505), and the second region was a 6 mm sphere centered on the peak voxel within this cluster (−45, −57, 54). The average PSC in each ROI for all nine conditions of interest are represented in Fig. 5. For each ROI, a two-way, repeated measures analysis of variance (ANOVA; 2×2 : source (perceived, imagined) by response (“perceived”, “imagined”)) was conducted on old items recognized as old (PP, PI, IP, IN) to test for main effects and interactions of source and response on brain activity. In order to control for false positives associated with multiple comparison testing, main effects and interactions within each region were tested against a false discovery rate (Behnamini & Hochberg, 1995) alpha level of $p < 0.05$ for 30 comparisons.

There was no evidence for a significant main effect of response or a significant source by response interaction in any of the 10 ROIs examined ($p > 0.05$). There were, however, several that demonstrated a significant main effect of source. Regions that were associated with significantly greater activity during source judgments of perceived compared to imagined events (PP+PI > IP+II) were all in the left hemisphere and included the anatomically defined angular gyrus ($F(1, 19)=8.91, p=0.008$) and IPL ($F(1, 19)=13.36, p=0.002$). In addition, both of the functionally defined ROIs from the successful retrieval contrast (PP+PI+IP+II > NN), including the full cluster as well as the 6 mm sphere centered at the peak voxel within this cluster demonstrated a significant main effect of source with a higher PSC associated with perceived compared to imagined events ($F(1, 19)=19.64, p < 0.001$; $F(1,19)=15.10, p < 0.001$, respectively). Two right hemisphere regions demonstrated the opposite main effect of source, with greater activity associated with imagined versus perceived events (IP+II > PP+PI). These included the right SMG ($F(1, 19)=11.253, p=0.003$) and the right SPL ($F(1, 19)=8.105, p=0.010$).

4. Discussion

According to source monitoring theory, retrieval of perceived and imagined events is qualitatively different (Johnson, Foley,

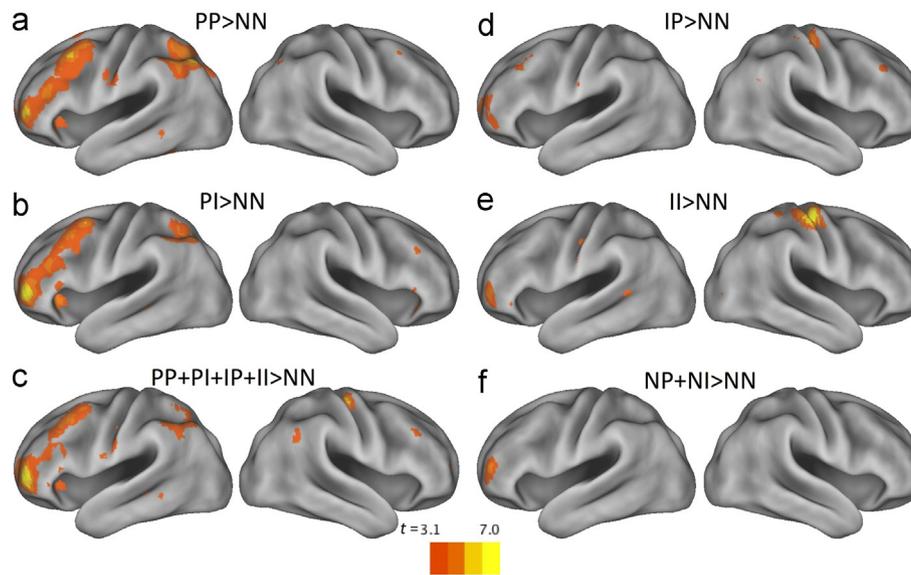


Fig. 4. Successful retrieval effects. Whole-brain, group-level comparisons [T] of each of the conditions that involved an old response to an old item (PP, PI, IP, II), as well as false alarms (NP+NI) contrasted with correct rejection (NN) trials. Voxels that exceeded the uncorrected threshold of $p < 0.001$ are displayed. Activations are mapped onto the inflated surface caret brain (CareT5). PP=perceive trial, perceived response; PI=perceive trial, imagined response; PN=perceive trial, new response; IP=imagine trial, perceived response; II=imagine trial, imagined response; and IN=imagine trial, new response.

Suengas, & Raye, 1988; Johnson et al., 1993; Mitchell & Johnson, 2009). Given this distinction, we hypothesized that brain regions recruited during reality monitoring judgments of studied items would differ depending on whether they were encoded through perception or imagery. The results confirmed our hypothesis. The whole-brain analysis revealed that several regions, including the left dorsolateral PFC and lateral PPC, exhibited significantly greater activity during reality monitoring judgments of perceived compared to imagined items. Activity in these regions also tracked well with item memory (hits > CR), but only for items that were perceived at encoding and not for those that were imagined. Given the ubiquity and robustness of parietal successful retrieval effects in the literature (Cabeza et al., 2008; Vilberg & Rugg, 2008; Wagner et al., 2005), the failure to detect any successful retrieval effects in the left lateral parietal cortex for imagined items when perceived items were associated with such a significant and widespread effect was rather striking. We were also surprised to find that lateral parietal activity did not vary according to source attribution or source accuracy. These findings may have important implications regarding theories of parietal contributions to recognition memory. A better understanding of what is driving these source-based differences in activity could provide insight regarding whether this region contributes more to the representation of stored mnemonic information or to cognitive processes necessary for successful memory retrieval.

In addition to the lateral PPC, regions of the left dorsolateral PFC exhibited source effects, responding more during source attributions of previously perceived compared to imagined events. Successful retrieval effects in this region were also more significant and widespread for items that were perceived compared to imagined at encoding. Similar to the lateral PPC, the dorsolateral PFC has been shown to exhibit successful retrieval effects in long-term memory studies (e.g. Achim & Lepage, 2005; Henson, Hornberger, & Rugg, 2005; Kahn et al., 2004; Morcom, Li, & Rugg, 2007) although these effects are typically observed in more ventral regions of PFC as well (e.g. Fließbach, Weiss, Klavary, Elger, & Webser, 2006; Kahn et al., 2004; Morcom et al., 2007). Similarly to the lateral PPC, whether these activations reflect the on-line representation of mnemonic information or the operations performed on such representations in order to guide behavior is

unclear (Curtis & D'Esposito, 2003; Han, Huettel, & Dobbins, 2009; Raposo, Han, & Dobbins, 2009; Wood & Grafman, 2003). Given its role in visual working memory (Bauer & Fuster, 1976; D'Esposito, Postle, & Rympa, 2000; Funahashi, Bruce, & Goldman-rakic, 1989; Müller, Machado, & Knight, 2002), source-based differences in dorsolateral PFC activity could reflect the maintenance of greater perceptual details associated with mnemonic representations of perceived compared to imagined events.

In addition to lateral PPC and dorsolateral PFC, posterior visual processing regions, including the left cuneus and fusiform gyrus were also associated with greater activity during source attributions of perceived compared to imagined events. Activation in these regions during retrieval likely reflects the reinstatement of processes or representations that were active during encoding. Consistent with past research (e.g., Ganis et al., 2006; Kosslyn et al., 1997; Stokes et al., 2009), both the left cuneus and fusiform gyrus, along with other posterior visual processing regions were associated with greater activity during encoding of perceived compared to imagined events. Cortical reinstatement models propose that patterns of activity elicited during encoding are stored in the hippocampus, and at retrieval, this pattern is reactivated in the hippocampus, leading to the reinstatement of activity in regions that were active during encoding (e.g., Marr, 1971; Norman & O'Reilly, 2003). Consistent with this theory, neuroimaging studies have demonstrated that brain regions that exhibited differences in activity during encoding of one stimulus class over another (e.g., words vs. pictures) showed a similar pattern of differential activity during retrieval (Kahn et al., 2004; Nyberg, Habib, McIntosh, & Tulving, 2000; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Woodruff, Johnson, Uncapher, & Rugg, 2005). Because visual processing regions, including the cuneus and fusiform gyrus, were more active during encoding of perceived compared to imagined events, differential activity in these regions during retrieval likely reflects the reinstatement of encoding activity. However, it is important to note that reinstatement cannot explain the source effects observed in dorsolateral PFC and lateral PPC during retrieval, as encoding activity in these regions did not vary as a function of source.

Source effects in the opposite direction were also evident at retrieval. Consistent with previous findings (Turner et al., 2008; Vinogradov et al., 2006), the medial anterior PFC was amongst the

Table 5

Whole-brain comparison of each of the conditions that involved an old response ("seen" or "imagined") to a studied trial (perceived or imagined) compared to correct rejections (PS, PI, IS, II vs. NN).

Anatomical region of center of mass	BA	x	y	z	t-Value	Cluster volume
PP > NN						
L inferior parietal lobe	40	-45	-57	51	7.10	1718
L postcentral gyrus	3	-27	-24	75	3.74	49
L middle frontal gyrus	10	-42	51	9	7.10	2353
R middle frontal gyrus	8	51	24	39	4.33	335
L inferior temporal gyrus	20	-60	-48	-9	3.88	45
L lingual Gyrus	17	-12	-99	-3	3.32	27
L inferior occipital gyrus	19	-39	-84	-3	2.77	14
L posterior cingulate gyrus	29	-3	-42	18	2.95	10
R cingulate gyrus	24	12	12	24	3.09	15
L putamen	-	-21	18	-15	2.87	12
L cerebellum	-	-45	-51	-21	3.90	186
R cerebellum	-	18	-54	-18	6.63	2288
PI > NN						
L inferior parietal lobe	40	-45	-57	51	6.54	372
R inferior parietal lobe	40	57	-54	42	3.97	34
R inferior parietal lobe	39	42	-63	48	3.27	16
L precuneus	7	-3	-72	51	3.59	59
L precuneus	19	-21	-81	48	3.09	12
L middle frontal gyrus	10	-39	51	6	7.15	1833
R middle frontal gyrus	8	48	27	42	5.13	184
R superior frontal gyrus	10	39	57	15	4.52	47
L middle temporal gyrus	-	-57	-39	-6	4.10	20
L cingulate gyrus	32	-12	30	27	3.79	14
L thalamus	-	-9	-6	3	4.92	141
R thalamus	-	30	-9	9	3.85	39
L putamen	-	-30	-18	-3	3.46	33
R cerebellum	-	9	-84	-24	5.20	559
R cerebellum	-	33	24	-3	3.60	21
L cerebellum	-	-9	-84	-27	3.30	14
IP > NN						
R supramarginal gyrus	40	60	-54	36	3.97	12
L/R medial frontal gyrus	9	0	39	27	4.22	35
L middle frontal gyrus	6	-45	18	48	4.75	60
R middle frontal gyrus	8	45	27	42	3.94	34
R middle frontal gyrus	9	33	36	24	3.91	10
R middle frontal gyrus	10	24	54	15	3.81	10
L superior frontal gyrus	10	-36	57	15	5.50	227
R superior frontal gyrus	6	15	24	60	3.86	11
R precentral gyrus	4	36	-24	54	5.25	81
R cingulate gyrus	32	15	27	27	4.71	31
II > NN						
R precentral gyrus	4	36	-24	54	7.63	235
L middle frontal gyrus	10	-39	48	6	4.92	113
L cingulate gyrus	31	-24	-24	42	4.12	19
L putamen	-	-30	-12	0	4.16	17
(NP + NI) > NN						
L Middle frontal gyrus	10	-42	48	15	5.06	37

Notes: x, y, z coordinates are in MNI space. Significant clusters are those that survived the FDR-corrected ($p < 0.05$) threshold. BA = Brodmann area; L = left; R = right; PP = perceive trial, perceived response; PI = perceive trial, imagined response; PN = perceive trial, new response; IP = imagine trial, perceived response; II = imagine trial, imagined response; IN = imagine trial, new response; NP = new trial, perceived response; NI = new trial, imagined response, NN = new trial, new response.

regions that exhibited significantly greater activity during source attributions of previously imagined compared to perceived events. In addition, a large cluster of voxels centered on the right postcentral gyrus, extending to the precentral gyrus, precuneus, SPL, and supramarginal gyrus was more active during source attributions of

previously imagined compared to perceived events. An examination of the beta values in this region revealed that this difference was actually due to a deactivation below baseline during retrieval of perceived events that was not evident during retrieval of imagined events. This deactivation during retrieval of perceived events may be explained in terms of a default mode network (DMN) account. The DMN consists of a set of functionally connected brain regions that consistently exhibit decreased neuronal activity when attention is focused on externally presented stimuli (Raichle et al., 2001; Shulman et al., 1997). Although its functional purpose is not well understood, many argue that the DMN is somehow involved in internally directed mental activity, such as self-referential mental activity (Gusnard, Akbudak, Shulman, & Raichle, 2001), stimulus independent thought (Mason et al., 2007), or self-projection (Buckner & Carroll, 2007). The DMN encompasses regions of the posterior parietal cortex that were found in the present study to be less active in the right hemisphere during retrieval of externally presented compared to internally generated events. It is unclear why the right lateral parietal cortex would be involved in these DMN processes, exhibiting decreases in activity during recognition of externally derived events, while the left lateral parietal cortex appeared to play more of a task-positive role. However, if it is the case that the left and right posterior parietal lobes play differential roles in representing memories of internally and externally generated information, then this could explain why old/new effects tend to be left lateralized in recognition memory studies (Guerin & Miller, 2009), which typically examine memory for externally presented stimuli.

In contrast to previous source monitoring studies (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Kahn et al., 2004; Kensinger & Schacter, 2006; Ragland, Valdez, Loughhead, Gur, & Gur, 2006), we did not find any evidence for a difference in lateral parietal activity according to source accuracy. For instance, the whole-brain comparison of correct source attributions (PP + II) to source misattributions (PI + IP) did not reveal any parietal regions that exhibited significantly different activity. There are several possibilities for why we did not find detect these effects. The majority of source memory studies reported in the literature involve the discrimination of two external (e.g., font color, size of presented stimulus) or two internal (e.g., pleasantness versus concrete/abstract judgment) sources of information. One possibility is that when the task involves discriminating between an internal and external source, parietal source accuracy effects may depend on the source of encoded stimuli. According to source monitoring theory, memories are attributed to the source class they most closely resemble. Therefore, if the role of the lateral parietal cortex is to represent the perceptually derived contextual details of encoded events, which typically pertain more to memories of perceptually derived than internally generated events, then activation in lateral parietal cortex during retrieval may serve to bias the source decision toward an external source attribution. This would benefit source accuracy performance for externally derived events, but hinder performance for imagined events. Support for this notion comes from two studies that examined source accuracy effects associated with perceived and imagined events. In each of these studies, source accuracy effects were reported for perceived events; however, for imagined events, the opposite effect occurred, with misattributions eliciting a greater parietal response than correct source attributions (Kahn et al., 2004; Kensinger & Schacter, 2006). In other words, for both perceived and imagined events, items that were attributed to an external source were associated with a greater response than items attributed to an internal source. In the present study, there were no significant differences in activity according to response for either perceived or imagined events. However, the general pattern of activity in left lateral PPC was consistent with these studies.

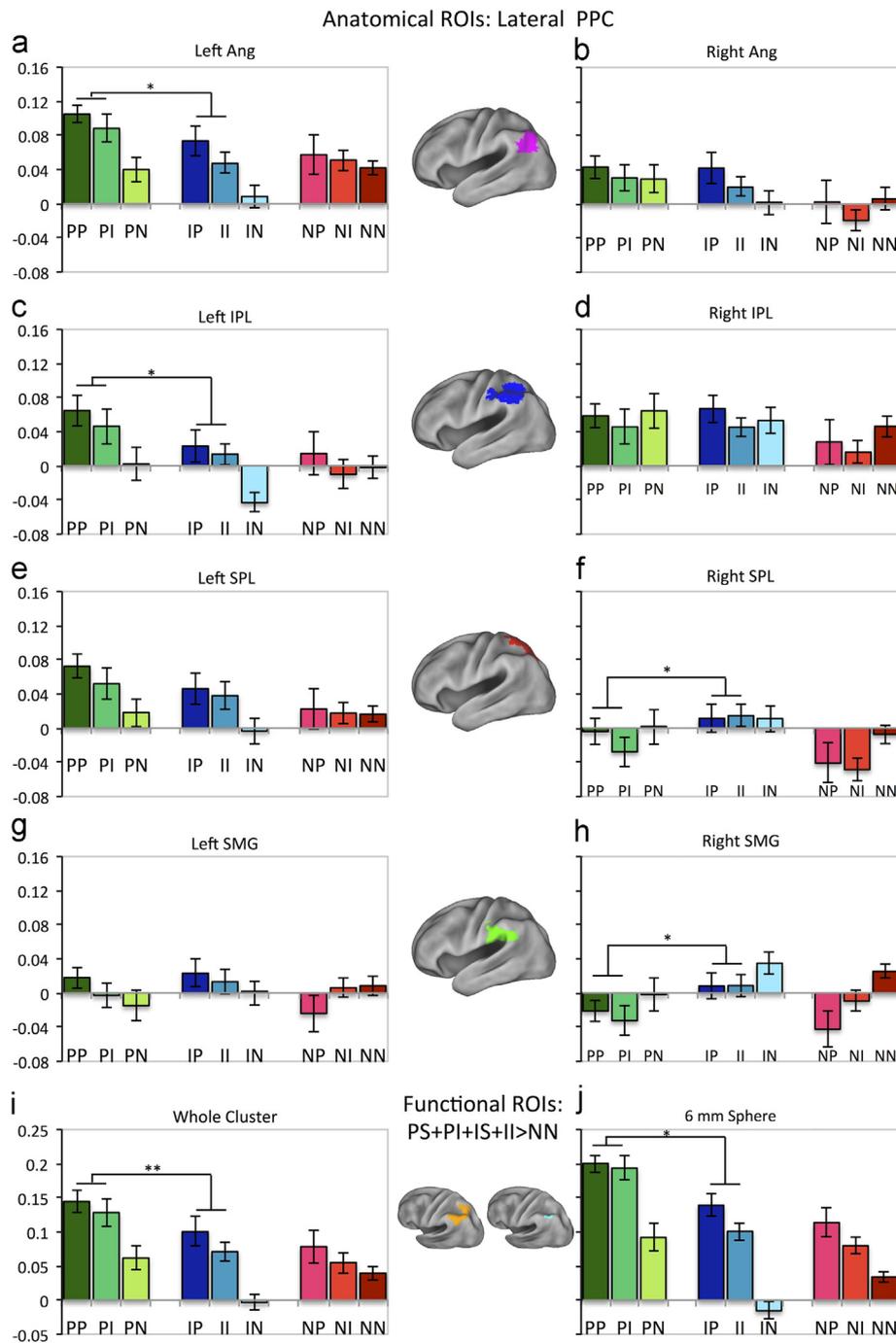


Fig. 5. Regions of interest analyses. Graphs represent the average percent BOLD signal change (Y-axis) for each of the source-response conditions compared to baseline. Significant main effects of source and response as well as interactions from the 2×2 source (perceived, imagined) by response (“perceived”, “imagined”) ANOVA that were significant at the FDR-corrected alpha level of $*p < 0.05$ and $**p < 0.01$ (corrected for 30 comparisons) are shown. Note that significance bars pertain only to the factors that were examined and not all nine conditions that are shown. PP=perceive trial, perceived response; PI=perceive trial, imagined response; PN=perceive trial, new response, IP=imagine trial, perceived response; II=imagine trial, imagined response; IN=imagine trial, new response. (a)–(h) are anatomically defined regions of interest defined by the AAL atlas. (i) and (j) are functionally defined regions of interest from the hits > CRs contrast (PP+PI+IP+II > NN): (i) all voxels within the left lateral parietal cluster that survived the whole-brain, FDR-corrected ($p < 0.05$) contrast threshold (j) 6 mm sphere centered at the peak of activation $\{-45, -57, 54\}$ for the contrast.

We also failed to replicate findings from previous studies that examined brain activity during reality monitoring discriminations. In these studies, several brain regions were more active when imagined events were misattributed to perception versus accurately attributed as imagined (IP > II; Kensinger & Schacter, 2006; Okado & Stark, 2003; Takahashi et al., 2002). Our failure to replicate this effect could be due to a key difference in the experimental design across studies. Several of these studies relied on a paradigm that involved a two-alternative forced-choice

decision as to whether perceived, imagined, and new items were either seen or not seen (Kensinger & Schacter, 2006; Okado & Stark, 2003). Hence, a “not seen” response was used to indicate both intended responses of “imagined” as well as “new.” Therefore, trials that involved a “not seen” response to imagined events, which were presumed to reflect accurate source attributions, also included forgotten imagined events. Thus, differences in activity associated with imagined events attributed as “seen” versus “not seen” may not necessarily reflect differences in processes

associated with false versus true remembering, but may instead reflect differences associated with accurate item memory versus forgetting. In a similar paradigm, participants made perceived/imagined judgments about encoded events (Takahashi et al., 2002). However, in this experiment, new items were not presented at test, which meant that participants were forced to guess the source of forgotten items. Given the evidence that there is a bias to attribute forgotten items to the source associated with poorer item recognition (Meiser, Sattler, & von Hecker, 2007) it is likely that this design was confounded by the disproportional inclusion of forgotten trials into one source response category. In the present study, participants were given three response options, which allowed for the separation of trials remembered as imagined from those that were thought to be new. When these trials were treated independently, we did not find evidence to support previous findings of differences in activity associated with imagined items that were falsely remembered as “seen” versus those that were accurately attributed as “imagined.”

Other possibilities for why we were not able to replicate source accuracy effects may be related to limitations in our experimental design. For instance, the difficulty of the task may have prevented the detection of differences in parietal activity according to accuracy/response. Participants were required to judge the source of a large number of test items (750) after a relatively long retention interval (24 h) which may have led to strong enough item familiarity to produce robust successful retrieval activity (PP+PI > NN), but not strong enough recollection to produce source accuracy effects (PP > PI). This is supported by the finding that successful retrieval effects in lateral PPC occurred in dorsal regions of the IPL and IPS that are thought to support familiarity-based retrieval, but not in ventral portions of the angular gyrus that are thought to support source recollection (Vilberg & Rugg, 2007, 2008; Yu, Johnson, & Rugg, 2012). Another potential limitation was that participants were not given the option of responding that they remembered an item as old but could not remember the source. Therefore, many source attributions likely reflected guesses. Had this response option been included, we could have distinguished intentional source attributions from guesses, and may have detected the source accuracy/attribution effects that have been previously reported in the literature.

The most striking result of this study in our mind was the disparity in recognition activity for perceived and imagined events in classic successful retrieval areas of the left lateral PPC. These results will need to be considered by extant models of parietal contributions to recognition memory. We will briefly discuss some of these hypotheses below.

The Attention to Memory (AtoM) hypothesis (Cabeza et al., 2008; Ciaramelli et al., 2008) suggests that dorsal and ventral regions of lateral PPC play complimentary roles in recognition memory, conceptually similar to their suggested relative contributions to the attentional system (Corbetta & Shulman, 2002). Dorsal PPC is thought to allocate top-down attentional resources to memory retrieval in order to facilitate strategic search and post-retrieval monitoring processes. In contrast, activity in ventral PPC is thought to reflect bottom-up attention to memory, contributing to direct retrieval, which occurs when there is a strong match between studied and retrieved information. In the present study, source effects were observed in top-down, dorsal regions of lateral PPC. Because reaction times did not vary according to source, and item memory was actually better for perceived than for imagined events, it doesn't seem likely that perceived events should require greater top-down attention than imagined events. Thus, the source-based differences in activity in the present study are difficult to explain with the AtoM model, unless it were accommodated to suggest that the lateral PPC focuses attention on the mnemonic representation of perceptually derived, but not

internally generated information. If this were the case than it may be that the medial anterior PFC plays a complimentary role in directing attention toward internal representations of imagined events, which is in line with studies demonstrating source effects in the opposite direction in this region (Dobbins & Wagner, 2005; Simons, Owen, Fletcher, & Burgess, 2005a; Simons, Gilbert, Owen, Fletcher, & Burgess 2005b).

The mnemonic accumulator model suggests that lateral PPC recognition activity reflects the accumulation of retrieved evidence that information is old (Kahn et al., 2004; Wagner et al., 2005; Wheeler & Buckner, 2003; Yonelinas et al., 2005). This hypothesis can explain the successful retrieval effects associated with perceived events in the present study (PP > NN, PI > NN). However, this hypothesis would again have to be accommodated to show that the lateral PPC accumulates evidence associated with perceptually derived, but not internally generated events. Another important prediction of the mnemonic accumulator model is that false alarms should be associated with a greater response than correct rejections. Although this finding has been reported previously (Kahn et al., 2004; Wheeler & Buckner, 2003), this effect was not replicated in the present study.

Several models suggest a representational role for the lateral parietal cortex in recognition memory. For instance, the episodic buffer model suggests that lateral PPC acts as a temporary storage system, supporting the maintenance and representation of the contextual details of episodic memories while a recognition decision is made (Vilberg & Rugg, 2008; Wagner et al., 2005). A related hypothesis, referred to as the cortical binding of relational activity (CoBRA) theory proposes that lateral PPC serves as a convergence zone where features of episodic memories that are represented in a distributed fashion throughout the cortex are integrated (Shimamura, 2011). These models can provide a good explanation for the source-based differences in retrieval activity observed in the present study. Because activity was found to vary depending on the nature of stored representations, this suggests that lateral PPC is involved in the representation of stored information. The lateral PPC may represent or bind the perceptually-based contextual details of episodic memories, while the representation or integration of cognitive operations may occur in other regions, such as the anterior medial PFC. The peak of source-based differences in activity in the present study was in the left IPS. This region has been shown to be more active when participants make source memory compared to item memory judgments (Dobbins et al., 2002; Dobbins & Wagner, 2005; Fan et al., 2003; Han et al., 2012), suggesting that it is involved in the maintenance or representation of the contextual details associated with an episodic memory. The results from the present study extend these findings by demonstrating that the IPS is particularly involved in the representation or binding of perceptually derived contextual details, and plays a far diminished role in representing internally generated contextual details. It is important to note that both the episodic buffer model as well as the CoBRA model propose that these maintenance/integration functions occur in the more ventral regions of the lateral PPC that have been associated with recollection-based retrieval (Hutchinson et al., 2012; Shimamura, 2011; Vilberg & Rugg, 2008), and not the more dorsal regions found in the present study to exhibit source effects. However, the results of the present study suggest that more dorsal regions of the lateral PPC around the IPS may also play a role in the on-line representation and integration of stored mnemonic information.

An alternative explanation for the source effects in lateral PPC is that activity in this region is tracking with the conservativeness of the response. On average, across subjects, “perceived” responses were more rare (and, therefore, more conservative) than “imagined” responses. Studies have demonstrated that parietal old/

new effects can track with the conservativeness of the subject's response when the probability that a given test item is old or new is varied (Aminoff et al. submitted for publication; O'Connor, Han, & Dobbins, 2010). In low target probability conditions, an "old" response to a studied item can activate these dorsal parietal and PFC regions that are commonly associated with cognitive control because the old item violates the probability, and therefore the expectation, that the item should be new (O'Connor et al., 2010). However, the patterns of brain activity observed in the present study are inconsistent with this explanation. First, if the source-based differences in activity were driven by the more conservative "perceived" attribution, then activity should vary according to source attribution, which we found no evidence for. In addition, imagined events attributed as "perceived" (IP) should be associated with a parietal response, whereas perceived events attributed as "imagined" (PI) should not. However, the results of both the successful retrieval and ROI analyses showed that PI trials activated lateral PPC, whereas IP trials did not. Therefore, it seems unlikely that the source effects can be explained by a conservativeness or expectancy violation account.

Another alternative explanation for the source-based differences in activity during retrieval is that they were a result of encoding specificity. The encoding phase involved the presentation of a word on each trial, followed by a picture depicting the word on half the trials (perceived condition), and an empty box indicating to subjects that they should visually imagine the cue word referent on the other half of trials (imagine trials). The test phase involved only the presentation of the cue word. It is possible, although we believe unlikely, given the time constraints and without any instruction to do so, that subjects were engaging in automatic visual imagery in response to the cue word at test. If this were the case, then the processing of test trials would have been more specific to the processing associated with encoding of items in the imagined compared to the perceived condition. Therefore, the retrieval of the perceived events may have been more difficult, leading to greater activation in cognitive control regions. However, there was no behavioral evidence for encoding specificity, i.e., there were no reaction time differences, and item memory was actually better for perceived compared to imagined events. Thus, it does not seem likely that the source effects in lateral PPC could be due to differences in the difficulty of making source attributions of perceived and imagined events due to encoding specificity.

In conclusion, the results of the present study demonstrated that a region of the lateral PPC known to be associated with successful recognition is more active during retrieval of memories that were derived through perception than generated internally. These results favor a representational account for this region, as the task demands did not vary as a function of source, whereas the nature of stored representations did. It could be the case that some other task demand or cognitive control issue that we have not identified may be producing these effects, without any discernible behavioral effect, but it seems likely that the representations themselves (either based on familiarity or contextual elements) are also playing a role. It also seems possible that neither a representational nor an attention/monitoring account can alone explain the functional contributions of the lateral PPC to recognition memory. In light of the plethora of conflicting evidence in the literature, we may need to look beyond the mutually exclusive models currently favored and consider models that can account for the seemingly disparate contributions of the parietal lobe to recognition memory (e.g., Nelson et al., 2010; Hutchinson et al., 2012). Regardless, the results of the present study demonstrate that activity in lateral PPC is highly sensitive to source, which must be taken into consideration by theories proposed to explain the role of this region in recognition memory.

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