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Influence of response bias and internal/external source on lateral posterior parietal successful retrieval activity



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ABSTRACT

In studies of recognition memory, regions of the lateral posterior parietal cortex exhibit greater activity (as indexed by the fMRI BOLD signal) during correct recognition of “old” (studied) items than correct rejection of “new” (unstudied) items. This effect appears to be source-sensitive, with greater activity associated with recognition of perceived than imagined events. Parietal successful retrieval activity also varies with response bias, or the tendency to be conservative about making “old” judgments. Here, we examined whether differences in response bias associated with recognition judgments of perceived and imagined events could account for source-based differences in LPPC activity. Participants perceived and imagined items in response to cue words and then at test, made recognition judgments in blocks that knowingly contained either a high or low proportion of old to new trials. While participants were indeed more conservative when making judgments about perceived than imagined events, the neuroimaging results demonstrated that response bias and source effects occurred in non-overlapping parietal regions. These findings suggest that source-based differences in LPPC activity cannot be explained by differences in response bias associated with recognizing perceived and imagined events.

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1. Introduction

Functional neuroimaging studies of recognition memory have consistently identified regions of the left lateral posterior parietal cortex (LPPC) that exhibit greater neural activity (as indexed by the fMRI BOLD signal) during recognition of previously studied items (hits) than during correct rejection of

new items (CRs), a finding referred to as the ‘parietal old/new’ or ‘parietal successful retrieval’ effect (for reviews, see Cabeza, 2008; Levy, 2012; Wagner, Shannon, Kahn, & Buckner, 2005). Additionally, there is evidence for a regional dissociation within LPPC such that activity in ventral regions is associated with recollection-based recognition, or recognition that involves retrieval of contextual details associated with the encoding event, whereas activity in more dorsal regions is

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associated with a-contextual, familiarity-based recognition (Kim et al., 2012; Rugg & Vilberg, 2013; Spaniol et al., 2009). A common approach for identifying the neural correlates of recollection and familiarity is to employ a source memory task, whereby studied items are presented from one of multiple ‘sources,’ (e.g., visual items presented on left or right side of screen, auditory words presented in male or female voice; e.g., Duarte, Henson, & Graham, 2011; Elward, Vilberg, & Rugg, 2014; Frithsen & Miller, 2014; Hayama, Vilberg, & Rugg, 2012; Yu, Johnson, & Rugg, 2012). At retrieval, activity elicited by source correct trials (i.e., items recognized along with source information) and source incorrect trials (the item is recognized but source information is forgotten) are thought to reflect recollection and familiarity processes, respectively. There is strong behavioral evidence suggesting that mnemonic information acquired through different sources is qualitatively distinct, and the processes involved in making source discriminations may depend on the category of sources being discriminated (Johnson & Raye, 1981; Johnson, Foley, Suengas, & Raye, 1988; Johnson, Hashtroudi, & Lindsay, 1993; Johnson, Raye, Foley, & Foley, 1981; Johnson, Raye, Foley, & Kim, 1982). For instance, memories from an external source, or for information acquired through perception, tend to contain greater sensory information than internally generated memories, or memories for thoughts and emotions, which contain greater information regarding the cognitive operations that were engaged during encoding (Johnson et al., 1981, 1982). Despite this phenomenological dissociation, in neuroimaging studies employing source memory tasks, the choice of which particular source manipulation to implement is seemingly made without regard to the possibility that the neural correlates associated with retrieving source information may differ depending on the category of retrieved source details (e.g., internal or external). In two recent studies, we examined how LPPC activity differed according to the internal/external (i.e., perceived/imagined) source of retrieved information (King & Miller, 2014; King, Schubert, & Miller, 2015). Indeed, we found that LPPC successful retrieval activity varied as a function of internal/external source, with retrieval of perceived, but not imagined events, eliciting a parietal successful retrieval response. These effects could not be explained by any discernable differences in behavioral performance associated with perceived and imagined events (e.g., source accuracy, item memory, reaction time). However, there is evidence that parietal retrieval activity varies with response bias, or the tendency to be conservative or cautious about judging items as old (Aminoff et al., 2015; O’Connor, Han, & Dobbins, 2010), and in our two prior studies, the designs did not allow for independent assessments of response bias associated with perceived and imagined events. Hence, the goal of the current study was to test whether differences in response bias could explain source-based differences in parietal retrieval activity.

Our two prior studies that utilized functional magnetic resonance imaging (fMRI) to examine neural correlates associated with retrieval of perceived and imagined events employed similar task paradigms (King & Miller, 2014; King et al., 2015). Each study involved an initial encoding phase, during which participants perceived and imagined images of objects in response to cue words, followed by a source

memory test, where participants made perceived/imagined/new judgments to old and new cue words. In both studies we found evidence for a source effect, such that words that were paired with a visually presented image at study were associated with greater retrieval-related activity at test than words presented with the cue to visually imagine the cue word referent. In addition, while perceived study items elicited a robust parietal successful retrieval response (as indexed by the “hits” or studied items recognized as old greater than correct rejections contrast), there was little evidence of parietal successful retrieval activity associated with imagined items. We refer to these findings as *source effects*, intending to imply a difference in the BOLD activity associated with retrieval of items encoded through different sources (perception vs imagination) rather than the *source accuracy effects* (difference in signal associated with source hit than source miss trials) commonly referenced in the literature.

In our original study (King & Miller, 2014), the task was sufficiently difficult and included a large enough number of trials to allow for examination of variations in brain activity according to both study source (perceived, imagined) and source attribution (perceived, imagined, new). Unlike in other studies (e.g., Duarte et al., 2011; Elward et al., 2014; Frithsen & Miller, 2014; Hayama et al., 2012; Yu et al., 2012), we failed to identify any source accuracy effects in LPPC (source “hits” > source “misses”). However, memory performance in this experiment was quite low, so this null result may have been due to the inclusion of ‘lucky guesses’ in the source hit conditions. In other words, we believe the difficulty of the task in the previous studies contributed to the failure to elicit any activity associated with recollection per se (which is typically assessed using a source accuracy contrast). However, there was a robust successful retrieval effect (identified by the hits > CR contrast), which, given the lack of source accuracy effects was likely driven by a combination familiarity-based recognition and recollection of non-criterial contextual information (i.e., contextual information that is non-diagnostic of the source, for instance, the color of the perceived/imagined object). Surprisingly, this recognition effect only occurred for the items that were originally perceived and not imagined – despite the lack of behavioral evidence to suggest that familiarity strength differed for perceived and imagined events. In this study, we also failed to identify any effects of source attribution. In other words, LPPC activity varied according to whether an item was perceived or imagined at encoding and not according to whether it was attributed to perception or imagination at test. These findings suggest that LPPC retrieval activity is better explained by the internal/external source through which information was encoded than by any processes that would lead to a particular memory judgment.

In a follow-up experiment, we tested whether source-based differences in LPPC retrieval activity could be explained by a difference in the perceptual vividness of memories of perceived and imagined events (King et al., 2015). Participants perceived and imagined both pictures (high vividness) and sentences (low vividness) in response to cue words prior to making perceived/imagined/new source judgments. Again, we found evidence for a main effect of source

(perceived > imagined) on LPPC activity. However, this effect could not be explained by a difference in the perceptual vividness of memories of perceived and imagined events. There was no evidence for an effect of vividness on LPPC retrieval activity. Similarly, the low vividness (sentence) perceive condition did elicit a robust parietal successful retrieval effect whereas the high vividness (picture) imagine condition did not. Combined, these two studies also allowed us to rule out a number of possible alternative explanations for observed source effects, as effects occurred despite variations in discernable patterns of behavior. For example, they occurred both when item memory performance was better and worse for perceived than imagined events, and when source accuracy performance and reaction time did and did not differ according to internal/external source. Hence, it appears, from these two studies, that LPPC source effects occur regardless of variations in study materials and behavioral performance.

Activity in regions of the LPPC that showed source effects in our two prior studies has also been shown to vary during recognition memory judgments depending on the probability that a test item is old or new (Aminoff et al., 2015; Herron, Henson, & Rugg, 2004; Vilberg & Rugg, 2009). In studies examining effects of target probability, participants studied lists of items, and then at test were shown old and new items in blocks consisting of either a high proportion of old items (high target probability) or a low proportion of old items (low target probability) and made either recognition or source memory judgments. A common finding across these studies was that successful retrieval effects in dorsal LPPC were significantly more pronounced in the low than high target probability conditions. Similar results were reported when target probability was manipulated on a trial-wise basis (Jaeger, Konkel, & Dobbins, 2013; O'Connor et al., 2010). Several explanations have been proposed to account for these findings. For instance, the enhanced response in the low target probability condition could reflect an expectancy violation, as old items that occur relatively infrequently violate the probability, and therefore the expectancy, that the item will be new (O'Connor et al., 2010). Alternatively, the difference in the magnitude of the parietal response may reflect differences in the saliency of the retrieval cues (Vilberg & Rugg, 2009). From this perspective, old items are considered targets, and the saliency of these targets is enhanced when their probability of occurrence is low.

A distinguishing feature of these studies relates to whether participants were made aware of the target probability manipulation. In Herron et al. (2004) and Vilberg and Rugg (2009), participants were not informed of the ratio of old to new items within each block and were specifically instructed to try not to allow any perceived differences in ratios to influence their recognition decisions. In contrast, in Aminoff et al. (2015) participants were explicitly informed of the proportion of old and new trials in each block and were told to try to use this information to inform their recognition judgment. Studies have demonstrated that conscious awareness of target probability causes participants to shift their response bias, adopting a more conservative response bias (i.e., responding “old” less frequently) when the probability that a given test item is old is low (Estes & Maddox, 1995;

Rhodes & Jacoby, 2007). Indeed, in previous fMRI studies, when participants were unaware of target probabilities, response bias did not differ across conditions (Herron et al., 2004; Vilberg & Rugg, 2009) whereas when they were aware of old/new ratios, participants were more conservative in responding “old” in the low target probability (i.e., infrequent old trials) than the high target probability (i.e., frequent old trials) condition (Aminoff et al., 2015; O'Connor et al., 2010). In addition to the increased activation in the superior parietal lobe observed in previous studies (Herron et al., 2004; Vilberg & Rugg, 2009), this conservative response bias in the low target probability condition was also accompanied by increased activation in the intraparietal sulcus (IPS). The authors suggested that the enhanced IPS activity associated with a conservative response bias was a reflection of the increased monitoring of decision evidence that occurs when participants were aware that the likelihood of an item being old was low (Aminoff et al., 2015).

The regions of the LPPC where activity varied according to response bias (Aminoff et al., 2015; Jaeger et al., 2013; O'Connor et al., 2010) were similar to those shown to exhibit an internal/external source effect (King & Miller, 2014; King et al., 2015). In our previous source memory studies, there were no consistent differences in the behavioral indices measured (e.g., item memory accuracy, source accuracy, reaction time) for perceived relative to imagined events that could account for source-based differences in activity. However, due to constraints in the design of these studies, we were unable to calculate measures of response bias separately for perceived and imagined items. Traditional measures of response bias are based on a comparison of the hit rate (i.e., proportion of studied items correctly recognized as old) to the false alarm rate (i.e., proportion of new items incorrectly endorsed as old; Green & Swets, 1966; Grier, 1971; Hodos, 1970; Luce, 1963). In each of our previous studies, because cue words corresponding to perceived and imagined events were intermixed with new words at test, we were unable to get independent estimates of the false alarm rates, and hence, the response biases, associated with perceived and imagined events.

It is possible that individuals are inherently more conservative when making recognition memory judgments about memories that were derived through perception than imagination. The majority of studies examining memory for perceived and imagined events have relied on a similar paradigm as our prior two studies, with perceived and imagined items intermixed with new items at test. Because this procedure does not allow for independent estimates of bias associated with each source, it is unclear whether people tend to adopt a different response bias when making judgments about perceived and imagined test items (Batchelder & Riefer, 1990; Bröder & Meiser, 2007). If this is the case, then differences in the conservativeness of the response bias could account for observed source-based differences in parietal activity. Here, we tested this hypothesis by scanning participants while they made old/new recognition memory judgments about previously perceived and imagined events under low (30%) and high (70%) target probability conditions. If source-based differences in parietal retrieval activity are due to a difference in response bias associated with perceived and

imagined events, we should expect to find that individuals are more conservative when making judgments about previously perceived than imagined items. In addition, there should be an overlap in the LPPC regions that exhibit source and target probability effects on parietal successful retrieval activity. Alternatively, if these effects occur in disparate parietal regions, this would suggest that a difference in response bias associated with memory judgments of perceived and imagined events cannot account for source-based differences in activity.

2. Materials and methods

2.1. Participants

Thirty-three participants (16 male, 17 female; ages 19–32 years, $M = 20.96$ years) from the University of California, Santa Barbara (UCSB) community volunteered to participate in response to an e-mail distributed to graduate students and staff. Participants were right-handed, native English speakers with normal or corrected-to-normal vision. Data from five participants were excluded from analysis due to excessive motion (>3 mm of motion in a single direction in a single experimental run; three participants), or an insufficient number of trials in one or more conditions of interest (<20 trials; two participants). Participants whose data contributed to the analyses presented here included 13 males and 15 females, aged 19–32 years ($M = 23.82$ years). All participants gave informed consent according to the procedures approved by the UCSB Institutional Review Board and were paid \$60 for their participation.

2.2. Stimuli and apparatus

Stimuli consisted of 800 word-picture pairs. Pictures were color photographs of objects on a white background that were resized to have a height of 300 pixels, with widths ranging from 150 to 716 pixels ($M = 319.16$, $SD = 69.9$). Words ranged from 2 to 20 characters ($M = 7.84$, $SD = 3.31$), and in most cases were a single word, but in some cases were two to three words (e.g., “baby bottle,” “spool of thread”). Pictures and words were presented on the center of the screen, and words were presented in 48-point Helvetica font. Words were presented in black font during the encoding phase and in red font during the retrieval phase. The square frame presented on imagine trials was a 300×300 pixel square box, centered on the screen.

For the first phase of the experiment, which took place outside of the scanner, stimuli were presented on a MacBook Pro and participants responded by pressing buttons on the keyboard. Response and reaction time data were recorded in MatLab. During the second phase, while participants were scanned, images were projected from the MacBook Pro onto a screen situated at the head of the scanner, made visible to the participants by a mirror mounted to the head coil. The presentation of stimuli was synchronized with the onset of each functional scan in order to assure accuracy of event timing. 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

A schematic representation of the task is depicted in Fig. 1. The two phases of the experiment were separated by 24 h. The first day of testing took place outside of the scanner. Prior to the experiment, participants were given instructions for the encoding task and were trained on a shortened version of the task. For the actual experiment, the encoding task included 400 trials that were separated into four blocks. On each trial a cue word was presented. On half the trials, a photo of an object that corresponded to the cue word was presented below the cue word (perceive trials), whereas on the other half of trials, a blank frame was presented which served as a cue for participants to visually imagine the cue word referent (imagine trials). Participants were instructed to either view the picture of the object (perceive trials) or visually imagine the cue word referent (imagine trials) and make a judgment regarding whether the object (in real life) was bigger than or smaller than a shoebox. Both the cue word and photo/box remained on the screen for 3 s and participants responded by pressing one of two buttons on the keyboard using their right hand middle and index fingers. Response mapping for the middle and index finger to indicate a ‘bigger than’ or ‘smaller than’ response was counterbalanced across subjects. Perceived and imagine trials were randomly inter-mixed within each block.

After a delay of 24 h, participants returned for the retrieval phase of the experiment. Participants were given instructions and completed a short practice of the retrieval task prior to entering the scanner. Anatomical (~10 min) and resting state functional connectivity (~8 min) scans were collected at the start of the scanning session. Participants were then scanned while performing the retrieval task, which was broken into eight functional runs. Within each block, words that were presented during the study phase (old words) were presented along with new words for 2s each, and participants were asked to make old/new recognition judgments for each item. Responses were made by pressing buttons on a button box inside the scanner. All participants responded using their right hand index and middle fingers but the mapping of the old/new response onto the middle/index finger was counter-balanced across subjects. Trials were separated into target probability blocks such that half of the trials occurred in high target probability blocks and the other half occurred in low target probability blocks. In high target probability blocks, 70% of the words were old and 30% were new, whereas in low target probability blocks, 30% of words were old and 70% were new. Participants were informed of the target probability prior to each block through both written instructions displayed on the screen, and verbal instructions, spoken by the experimenter and transmitted through the intercom system. Additionally, for the duration of each block the words “likely old” or “likely new” were displayed at the top of the screen serving as a reminder of the current target probability condition. Prior to the retrieval phase, participants were told that if they were fairly certain about whether an item was old or new they should respond accordingly; however, if they were somewhat uncertain about item history, then relying on the target probability to guide their decision would be advantageous.

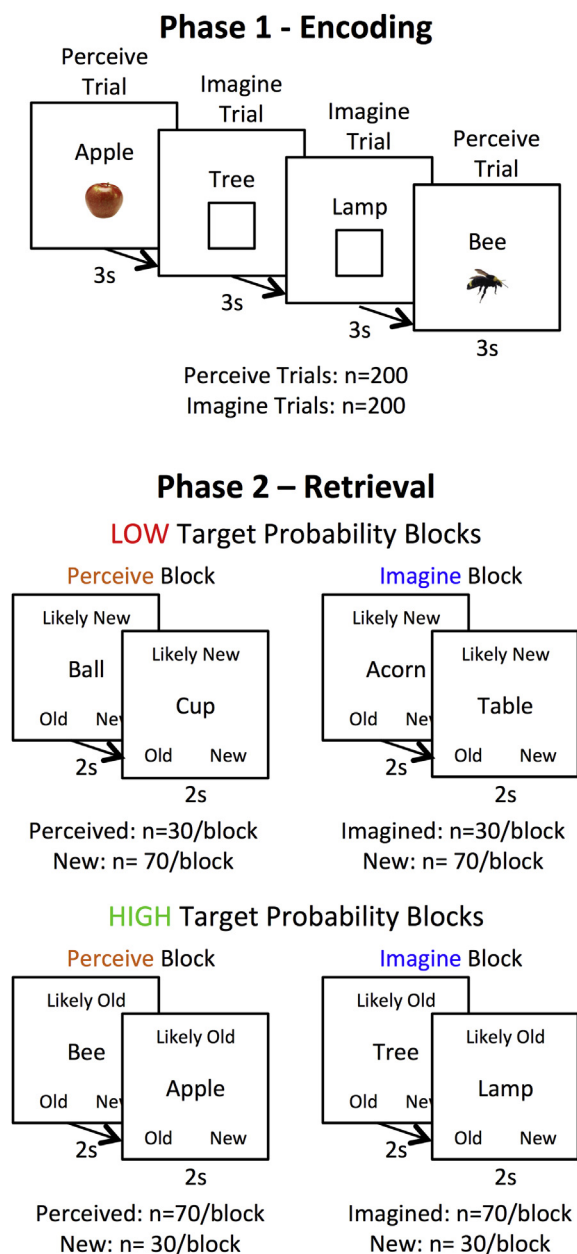


Fig. 1 – Schematic depiction of experimental task and procedure. During Phase 1 (Encoding), which took place outside of the scanner, Perceive and Imagine trials were randomly intermixed with jitter trials across four encoding conditions. Participants were instructed to view images on perceive trials, and to create mental images of the cue word referents on imagine trials, and then make a size judgment about the perceived/imagined object. Phase 2 (Retrieval) took place in the scanner and immediately followed Phase 1. Old and new words were presented and randomly intermixed with jitter trials. Phase 2 was separated into eight experimental blocks, with two blocks for each of four experimental conditions. The conditions were based on a 2×2 design and differed with respect to the source of old items (perceived, imagined) presented in each block and the ratio of old to new items (high = 70 old/30 new, low = 30 old/70 new) in each block. The order that conditions occurred was determined randomly. The task was to make an old/new recognition memory judgment.

In addition to blocking trials by target probability, trials were blocked by source such that all of the old words presented within a single retrieval block were either in the perceive or imagine condition during the encoding phase. The reason for separating perceived and imagined events was to get independent estimates of the false alarm rates associated with items from each source. If trials from two sources are intermixed, then the false alarm rate, or the tendency to call new items old, cannot be assessed independently for each source, and any differences in measures of response bias (e.g., c measured according to Signal Detection Theory) are only a reflection of differences in hit rates associated with perceived and imagined events. Through behavioral piloting we learned that when trials were blocked by source and participants made source judgments (e.g., perceived/imagined/new) rather than old/new judgments they quickly learned that all old trials within a block were either perceived or imagined. Hence, we asked participants to make old/new judgments instead of source judgments. However, it is likely that some participants were still aware of the source blocking.

To summarize the design, retrieval blocks were created according to $2 \times 2 \times 2$, mixed-block/event-related design, where source (perceive, imagine) and target probability (high, low) were blocked, resulting in four different conditions (perceive-high, perceive-low, imagine-high, imagine-low), each of which were repeated twice. Item history of the cue word (old, new) was randomly intermixed within each block. The order of the blocks was determined randomly for each subject. Each block consisted of a total of 100, 2s trials intermixed with 50, 2s jitter trials that were introduced for statistical modeling purposes. Jitter trials involved the presentation of a central fixation cross and did not require a response from participants. The optimal sequence for the order that trials were presented according to 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. A new sequence was generated for each subject, for each experimental run. For both the encoding and retrieval phases, sequences were generated with the additional constraint that any given trial type (i.e., perceive or imagine for the encoding phase; old or new for the test phase) could not be presented more than four times consecutively. Each run lasted roughly five and a half minutes. Following the retrieval phase of the experiment, a second resting state scan (~8 min) and a diffusion tensor imaging (DTI) scan (~5 min) were collected. The total time in the scanner was roughly 90 min.

2.4. fMRI methods

2.4.1. Data acquisition

Imaging was performed at the UCSB Brain Imaging Center on a 3T Siemens TIM Trio scanner with a standard 12-channel coil. Prior to functional scanning, an anatomical scan was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; TR = 2300 msec; TE = 2.98 msec; FA = 9°; 160 sagittal slices; 1.1 mm thick;

256 × 256 matrix). Each of the eight task functional runs included a series of 164 T2*-weighted whole-brain echoplanar images (EPI; 2000 msec repetition time (TR), 30 msec 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). The first four volumes of each block were discarded to allow for tissue magnetization prior to starting the task.

2.4.2. Preprocessing

Standard preprocessing was conducted using SPM8 (<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 were used to exclude subjects with excessive motion (>3 mm in any direction within an experimental run). 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 SPM8 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 to reduce noise.

2.4.3. Statistical modeling

Time-series data were modeled and estimated using a general linear model (GLM) in SPM8. At the individual subject level, the hemodynamic response to nine different events was estimated. Events included trials eliciting a correct response to each of the eight conditions, comprised according to a 2 × 2 × 2, source (perceive, imagine), by target probability (high, low), by item history (old, new) design. The last event included trials where an incorrect response, no response, or multiple responses were given. The neural response elicited on each trial was modeled as a delta function corresponding to the onset of each trial. Delta functions were convolved with a canonical hemodynamic response function (HRF) to model the predicted BOLD response. Temporal and dispersion derivatives of the canonical HRF associated with each event were also modeled. In addition, six regressor covariates representing the motion-related variance in the data (three for rigid-body translation and three for rotation) and regressors modeling the separate scan sessions were included in the model as covariates of no interest. An autoregressive AR(1) model used globally over the whole brain was applied during parameter estimation to correct for time-series correlations in the data.

Following estimation of the first level models, contrast images comparing activity associated with hits (correctly identified old items) to activity associated with correct rejections (correctly identified new items) for each of the source/target probability conditions were constructed. To examine how successful retrieval activity (hits > CRs) varied according to source and target probability, we entered first level contrast images into a second-level, random effects,

repeated measures factorial analysis, treating participants as the random variable. The analysis was based on a 2 × 2 source (perceived, imagined) by target probability (high, low) design. The covariance components were estimated with Restricted Maximum Likelihood (ReML) in SPM8 and used to adjust the statistics and degrees of freedom during inference to account for within-subjects correlation of measures due to the repeated measure design.

2.4.4. Sustained source and target probability effects

Although the current study was not intended to be analyzed according to a block-design, we took advantage of the clustering of trials into blocks that varied according to source (perceive, imagine) and target probability (high, low) to examine sustained effects of source and target probability on retrieval-related activity (ignoring item history (old, new) and recognition response (“old”, “new”). To do this, we estimated the hemodynamic response for four conditions of interest (perceive-high, perceive-low, imagine-high, imagine-low). The neural response elicited by each condition was modeled as a boxcar function, beginning at the onset of the first trial of each block, and lasting the duration of the block. Boxcar functions were convolved with a canonical HRF to model the predicted BOLD response. Contrast images of activity associated with each condition relative to baseline were brought to a second-level analysis, where a 2 × 2 ANOVA tested for main effects and an interaction of source and target probability on sustained activity during a retrieval task.

3. Results

3.1. Behavioral results

Memory performance was assessed according to Signal Detection Theory (Green & Swets, 1966). Sensitivity (d') and criterion (c) were calculated separately for each source/target probability condition. Two-way, within-subjects analyses of variance (ANOVAs) were conducted to test for main effects and interactions of source and target probability on item memory (d'), response bias (c), and reaction time (RT). Means and standard deviations for each of these behavioral indices are presented in Table 1 and Fig. 2. In the case of a significant

Table 1 – Mean and (standard deviation) behavioral measures across source/target probability conditions.

Behavioral index	Low target probability		High target probability	
	Perceive	Imagine	Perceive	Imagine
Item memory (d')	1.16 (.49)	1.44 (.53)	1.11 (.44)	1.18 (.54)
Response bias (c)	.47 (.28)	.33 (.26)	.04 (.28)	-.16 (.30)
Hit rate	.54 (.12)	.64 (.14)	.69 (.10)	.76 (.11)
FA rate	.17 (.10)	.16 (.07)	.29 (.14)	.35 (.14)
Reaction time	1.17 (.10)	1.13 (.10)	1.13 (.10)	1.08 (.11)

Note. Reaction times are in seconds and reflect trials that elicited a correct response (hits) only.

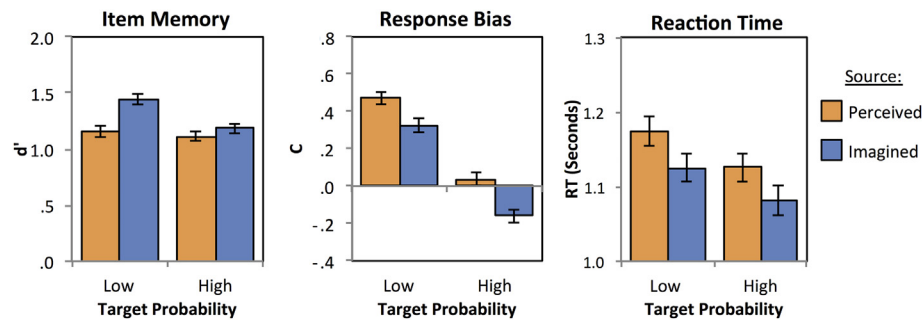


Fig. 2 – Behavioral performance across source and target probability conditions. Item memory (d') and response bias (c) were calculated according to Signal Detection Theory. Average reaction times reflect correct responses only. Error bars are the standard error of the mean. See Results – Behavioral Results for the results of the statistical analyses comparing each of the behavioral measures across source and target probability conditions.

interaction, post-hoc comparisons were conducted using multiple paired-samples t -tests tested against a Sidak corrected ($c = 6$ comparisons) family-wise alpha level of .05 ($\alpha = .0085$).

The results of the first ANOVA revealed that there was a significant source by target probability interaction on item memory [d' ; $F(1, 27) = 4.42, p = .045$]. Post-hoc analyses demonstrated that for the low target probability condition, item memory was significantly better for imagined compared to perceived events [$t(27) = 3.23, p = .003$], whereas in the high target probability condition, item memory did not differ according to source ($p > .05$). Item memory for the low probability imagine condition was also better than both the perceive [$t(27) = 4.27, p < .001$] and imagine [$t(27) = 4.05, p < .001$] high target probability conditions. There were no other differences in item memory across source/target probability conditions.

With respect to response bias, there were significant main effects of both target probability [$F(1, 27) = 62.06, p < .001$] and source [$F(1, 27) = 24.24, p < .001$], but no significant interaction. As expected, participants were significantly more conservative in the low target probability conditions ($M = .39, SD = .40$) than the high target probability conditions ($M = -.07, SD = .30$). Participants also made more conservative judgments in the perceive ($M = .26, SD = .35$) than the imagine ($M = .08, SD = .37$) conditions.

Reaction times for trials eliciting a correct response were compared across source and target probability conditions. There were significant main effects of both source [$F(1, 27) = 4.99, p = .034$] and target probability [$F(1, 27) = 23.39, p < .001$] on reaction time. Responses were significantly slower in low target probability ($M = 1.16, SD = .10$) than the high target probability condition ($M = 1.14, SD = .10$) and responses to imagined events ($M = 1.16, SD = .11$) were slower than responses to perceived events ($M = 1.14, SD = .10$).

3.2. Whole-brain fMRI results

Successful retrieval (hits > CRs) contrast images from the first level analysis were entered into a second level random effects, repeated measures factorial analysis to test for main effects and interactions of source and target probability on successful retrieval activity. Contrast images depicting successful retrieval activity associated with each of the four

conditions of interest were constructed (Fig. 3, Table 2). Contrast images were also constructed to depict main effects of source and target probability (Fig. 4, Table 3) on successful retrieval activity. To determine the voxel extent threshold that would result in a cluster-wise threshold of $p < .05$ we estimated the spatial autocorrelation and smoothness of our data using the 3dFWHMx program implemented in AFNI, then entered these parameters into a Monte-Carlo simulation (https://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html). Based on the results of this procedure, images were thresholded at $p < .001$, uncorrected, with a 68-voxel extent threshold. Anatomical locations of the peak voxel within each supra-threshold cluster are listed in Tables 2 and 3.

3.2.1. Successful retrieval effects across source and target probability conditions

We examined successful retrieval activity, or voxels where the BOLD signal was greater for correct recognition of old items (hits) than correct rejection of new items (CRs), separately for each of the four source/target probability conditions (Fig. 3, Table 2). For the low target probability/perceive condition (Fig. 1a), there was widespread successful retrieval activity throughout frontal and parietal regions. Parietal activity occurred bilaterally, with the peak of activity centered on the inferior bank of the left superior parietal lobe (SPL), extending to left and right IPS, angular gyrus (AnG), supramarginal gyrus (SMG), postcentral gyrus, paracentral lobe, and precuneus. Bilateral prefrontal regions also exhibited successful retrieval effects, including posterior medial prefrontal cortex (MPFC), anterior and posterior ventrolateral and dorsolateral prefrontal cortex (VLPFC and DLPFC), and precentral gyrus. Successful retrieval activity in posterior regions of the brain were observed in lingual gyrus, fusiform gyrus, cuneus, and the inferior, middle, and superior temporal and occipital gyri. Other regions that exhibited successful retrieval activity included parts of the cingulate gyrus, parahippocampal gyrus, insula, caudate, putamen, thalamus, and cerebellum.

In contrast to the widespread activation detected in the low probability/perceive condition, the extent of regions exhibiting this effect in the low target probability/imagine condition was far more limited (Fig. 1b). Voxels exhibiting this effect included a cluster in left LPFC, with the peak of activity in SPL,

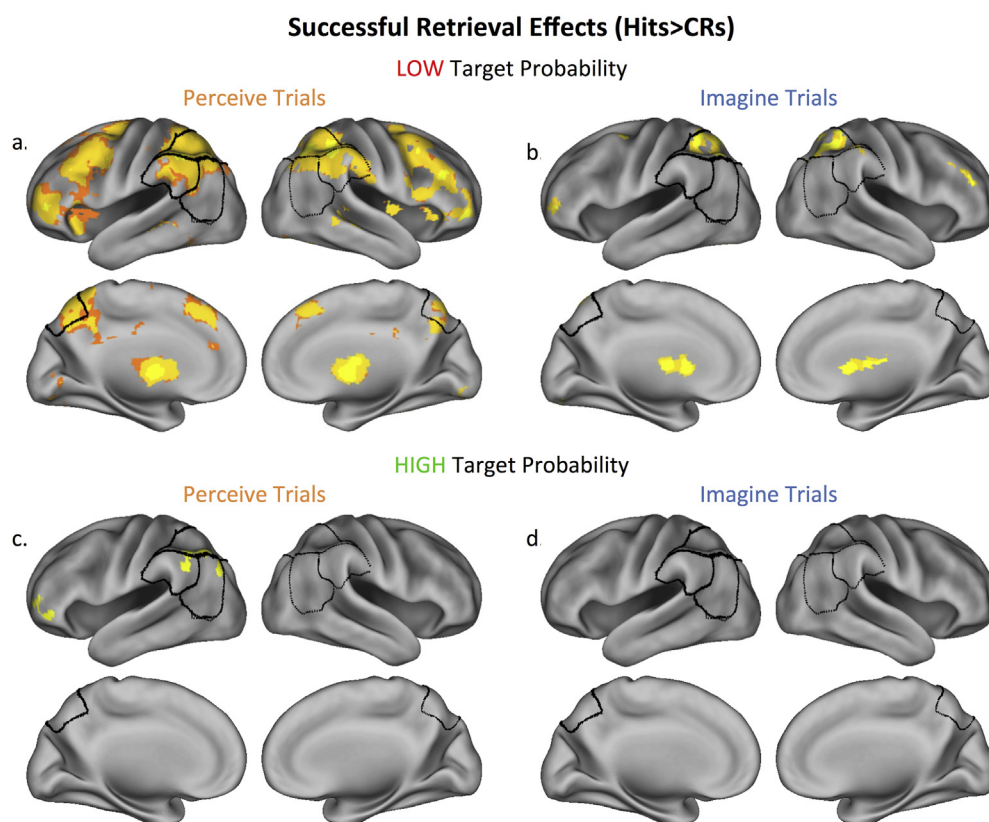


Fig. 3 – Successful retrieval effects across source and target probability conditions. Brains represent the group-level successful retrieval effects (Hits > correct rejections (CRs)) for each source (perceive, imagine) and target probability (high, low) condition. (a) perceive/low target probability; (b) imagine/low target probability; (c) perceive/high target probability; (d) imagine/high target probability. Voxels that exceeded the uncorrected height threshold of $p < .001$ and the voxel extent threshold of $k = 68$ are displayed on the inflated surface caret brain (Caret5) and depicted here from the lateral and medial views. The borders of Brodmann areas 7 (dorsal), 39 (ventral posterior), and 40 (ventral anterior) are shown in black.

extending to the IPS and precuneus. In right LPPC, a cluster of voxels centered on the SPL and extending to IPS exhibited a successful retrieval effect. Several small clusters of voxels exhibited a successful retrieval effect in VLPFC, bilaterally. Other regions exhibiting this effect included the right caudate and bilateral cerebellum.

In the high target probability/perceive condition (Fig. 1c), successful retrieval activity was detected in the left LPPC, with the peak of activity in the IPS, extending to the ventral SPL, as well as superior portions of the AnG and SMG. A small cluster of voxels in left VLPFC also showed this effect. There were no clusters of voxels that exhibited a significant successful retrieval effect in the high target probability/imagine condition (Fig. 1d).

3.2.2. Main effect of source on successful retrieval activity

We examined the main effect of source on successful retrieval activity (Fig. 4a, Table 3) and to determine the direction of effects, we inclusively masked the main effect with each of the directional effects (i.e., main effect of source was masked by perceived > imagined and imagined > perceived SPMs; mask threshold of $p < .001$, uncorrected). Two clusters of voxels exhibited a significant main effect of source, and in each case this was due to greater activity associated with

retrieval of perceived than imagined events (no voxels exhibited greater activity for imagined than perceived events). A cluster in left LPPC demonstrated this effect, with the peak of activity in the SMG, extending to the ventral bank of the IPS and the anterior portion of the AnG. In the right LPPC, a portion of the anterior SMG exhibited a main effect of source.

3.2.3. Main effect of target probability on successful retrieval activity

We also investigated whether there were brain regions that demonstrated a significant main effect of target probability on successful retrieval activity. Again, to determine the direction of significant effects, we inclusively masked the main effect contrast with directional contrasts (i.e., main effect of target probability was masked with low probability > high probability and by high probability > low probability; mask threshold of $p < .001$, uncorrected). Several clusters of voxels exhibited a significant main effect of target probability, and in each case this was driven by greater activity associated with the low than the high probability conditions (Fig. 4b, Table 3). In the left LPPC, a cluster of voxels exhibiting this effect peaked in the SPL and extended to the anterior portion of the IPS and SMG. In the right LPPC, similar regions demonstrated this effect, with activity peaking in the SPL and extending to

Table 2 – Whole-brain successful retrieval effects by source and target probability condition.

Region	# vox	Peak T	Coords (x, y, z)		
Perceive, low target probability (Hits > CRs)					
L IPS	4268	6.93	−39	−61	55
L/R PCC		4.04	0	−19	31
R SMG		4.38	63	−19	25
R AnG		6.28	36	−58	52
R MTG	151	5.41	54	−37	−5
L Thalamus	5955	7.80	−6	−1	7
R VLPFC		6.29	48	50	−8
L VLPFC		6.11	−45	47	4
L mPFC		5.07	−3	35	52
R DLPFC		5.73	48	11	43
L Precentral Gy.		6.25	−48	5	40
R Insula		3.73	42	−25	−5
R Cerebellum	1704	6.30	9	−79	−26
L MTG		5.28	−63	−40	−8
L Cerebellum	218	4.63	−24	−37	−29
Imagine, low target probability (Hits > CRs)					
L SPL	448	5.07	−36	−67	55
R SPL	438	5.18	39	−52	64
L VLPFC	88	4.15	−42	53	−2
R VLPFC	82	4.99	45	41	25
L Precentral Gy.	68	5.18	−30	−1	58
R Caudate	396	5.12	9	11	7
L Cerebellum	603	4.87	−33	−64	−35
R Cerebellum		4.12	33	−70	−29
Perceive, high target probability (Hits > CRs)					
L IPS	280	4.50	−36	−67	58
L VLPFC	104	4.16	−48	47	−11
Imagine, high target probability (Hits > CRs)					
None.					

Notes: Peak T-values and coordinates refer to peak of activated cluster. Clusters of >21 contiguous voxels are reported. For clusters of >500 contiguous voxels, local maxima >50 mm apart are reported. Number of supra-threshold voxels in cluster (# vox), T value of the main effect (Peak T), coordinates of the peak voxel within the cluster in MNI stereotaxic space (Coords [x, y, z]). Correct rejections (CR), left (L), right (R), bilateral (B). Angular Gyrus (AnG), Inferior parietal lobe (IPL), Intraparietal Sulcus (IPS), Medial Prefrontal Cortex (mPFC), Middle Temporal Gyrus (MTG), Posterior Cingulate Cortex (PCC), Superior Parietal Lobe (SPL), Supramarginal Gyrus (SMG), Ventrolateral Prefrontal Cortex (VLPFC).

the IPS and dorsal portions of the SMG and AnG. Other areas that exhibited this effect included left precentral gyrus, left thalamus, and the cerebellum bilaterally.

3.2.4. Source by target probability interaction and overlap of source and target probability effects

In addition to testing for main effects of source and target probability, we also examined the source by target probability interaction. There were no voxels that demonstrated a significant source by target probability interaction. We also examined whether there were any regions that demonstrated effects of both source and target probability by inclusively masking the main effect of source with the main effect of target probability (inclusive mask threshold of $p < .001$, uncorrected). No voxels exhibited main effects of both source and target probability. We examined this overlap at a more relaxed threshold of $p < .005$, uncorrected, with an inclusive

mask threshold of $p < .005$. At this reduced threshold, there was still little overlap of source and target probability effects in LPPC. One cluster of 91 voxels in very anterior SPL/post-central gyrus exhibited both source and target probability effects (Supplementary Fig. 1).

3.2.5. Sustained source and target probability effects

Although the current study was not designed to be analyzed according to a block-design, it was the case that trials were separated into blocks that varied according to both encoding source (perceived, imagined) and target probability (high, low). Hence, by ignoring both item history (old, new) and recognition judgment response (“old”/“new”), we could test for “sustained” effects of source and target probability. In other words, the design allowed us to test whether the activity in LPPC (and other regions) was differentially modulated by sustained orientation to different aspects of potential memories, regardless of what was remembered, per se. The results of this analysis revealed that there were no clusters of voxels that exhibited main effects or an interaction of source and target probability on sustained retrieval-related activity. This null finding suggests that activity did not vary according to whether individuals were oriented toward making responses to trials that varied with respect to the proportion of old/new trials within a retrieval block, or the perceived/imagined source of old items within a retrieval block. However, as the design of the study was not optimized for a block-design analysis, these null findings should be interpreted with caution.

3.3. Comparing effects with previous studies: Regions of Interest (ROI) analyses and across-study overlap map

To compare source effects observed in the current study to those observed in our previous studies we conducted several ROI analyses examining how successful retrieval activity varied as a function of source and target probability in regions exhibiting source effects in each study. We drew 5 mm sphere ROIs around the voxel that showed the peak source effect in each study and extracted parameter estimates of successful recognition activity (Hits > CRs) associated with each source/target probability condition. Separate 2×2 , source (perceived, imagined) by target probability (low, high) ANOVAs tested for main effects and interactions of source and target probability. To control for multiple comparisons, effects were tested against a Sidak corrected ($c = 3$ comparisons) family-wise alpha level of .05 ($\alpha = .017$). Results of the ROI analyses are plotted in Fig. 5 (ROI1 is from King & Miller, 2014, ROI2 is from King et al., 2015, and ROI3 is from the current study). There was no evidence for a significant source by target probability interaction on successful retrieval activity in any ROI. Unsurprisingly, for the ROI that was centered on the peak source effect from the current study (ROI3), there was a main effect of source with greater activity associated with perceived than imagined items [$F(1,27) = 17.66$, $p < .001$]. For the other two ROIs, which were centered on the peak source effect from our two prior studies, there were trends toward main effects of source, but they did not reach statistical significance after the alpha levels were adjusted to control for multiple comparisons [ROI1: $F(1,27) = 6.31$, $p = .018$; ROI2: $F(1,27) = 5.41$,

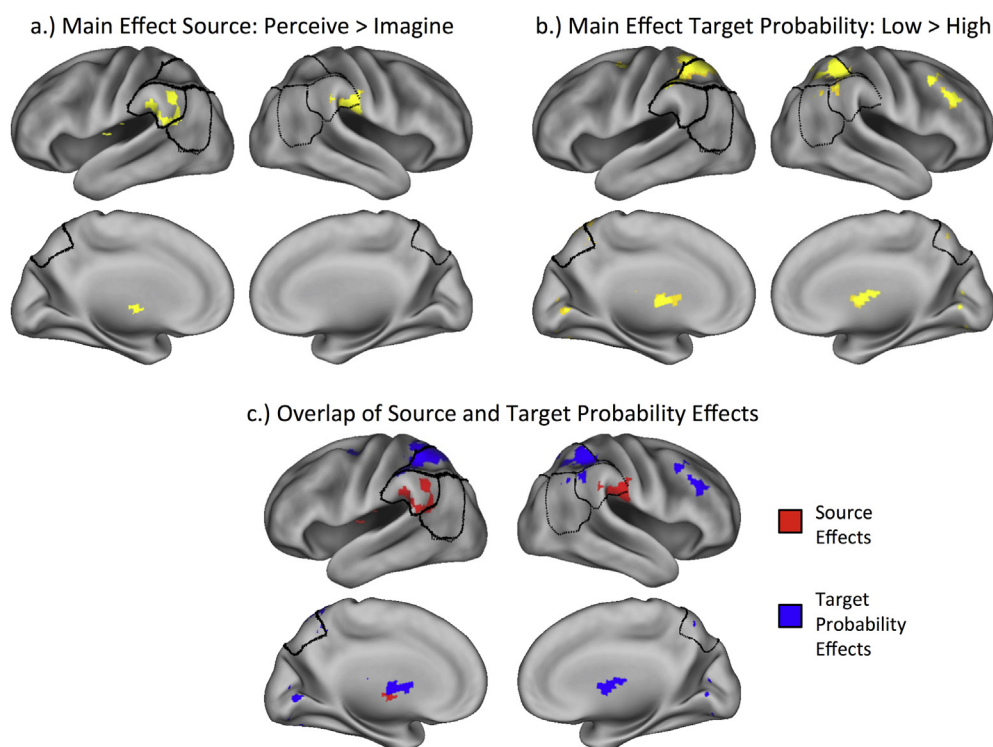


Fig. 4 – Main effects of source and target probability. Activation maps represent voxels that exhibited a significant main effect of source (a) or target probability (b) on successful retrieval activity (Hits > CRs). Voxels that exceeded the uncorrected height threshold of $p < .001$ and a voxel extent threshold of $k = 68$ are displayed on the inflated surface caret brain (Caret5) and depicted here from the medial and lateral views. Both source and target probability main effect maps were inclusively masked (mask threshold of $p < .001$) by the simple effect contrast maps to determine the direction of the effects. For the main effect of source (a), only the map masked by the perceive > imagine simple effect is shown here, as masking with the opposite contrast (imagine > perceive) did not result in any suprathreshold voxels. Similarly, for the main effect of target probability, only results of inclusively masking with the low > high simple effect is shown here, as masking with the opposite effect (high > low) did not result in any suprathreshold voxels. Main effects of source (red) and target probability (blue) are overlaid on the same surface in (c). To determine whether there was an overlap of these effects, we inclusively masked the main effect of source with the main effect of target probability, but this did not result in any suprathreshold voxels. There were also no clusters of voxels that exhibited a significant source by target probability interaction.

$p = .028$]. There was evidence for a main effect of target probability in only one of the ROIs that were tested [ROI2; $F(1,27) = 8.65$, $p = .007$].

To further compare the source and target probability effects observed across studies, we created an overlap map where regions exhibiting source effects in each study and any overlap of effects were represented by different colors (Fig. 6). There was substantial overlap in source effects in our prior two studies (King & Miller, 2014; King et al., 2015) with activity centered in the IPS. However, regions exhibiting a source effect in the current study did not overlap with regions that showed this effect in our previous studies. Source effects in the current study were in more ventral anterior LPPC, predominantly in SMG. Potential explanations for this deviation in the LPPC regions that exhibited source effects are proposed in the Discussion. We also plotted the target probability effects from the current study on the overlap map. As is evident in the figure, there was very little overlap in regions exhibiting the target probability effect in the current study and regions exhibiting a source effect in any of the three experiments.

3.4. Control analyses

3.4.1. Statistically controlling for differences in measures of performance

To further explore whether source effects were driven by differences in response bias, we ran a second-level ANCOVA model, entering individual subject estimates of criterion (c) for each of the different source and target probability conditions. If source effects were due to differences in criterion associated with the perceived and imagined conditions, entering criterion as a regressor in the model should eliminate or reduce the magnitude of source effects in LPPC. However, partialing out effects of criterion had very little impact on the main effect of source across the whole brain. Of interest, the cluster in left LPPC was again identified, with the same peak of activity (-48 , -52 , 28) and similar voxel extent ($k = 181$ voxels compared with $k = 160$ voxels when criterion was not entered into the model). Entering individual subject estimates of criterion associated with each source/target probability condition did, however, eliminate all previously observed effects of target

Table 3 – Whole-brain main effects of source and target probability.

Region	# vox	Peak F	Coords (x, y, z)			Dir
Main effect source						
L SMG	160	22.47	−48	−52	28	P > I
R SMG	108	21.17	60	−25	28	P > I
Main effect target probability						
L SPL	426	29.41	−42	−46	58	Lo > Hi
R SPL	250	26.56	42	−49	61	Lo > Hi
L Precentral Gy.	97	25.68	−33	−4	61	Lo > Hi
L Thalamus	128	23.66	−6	−4	10	Lo > Hi
L Cerebellum	343	24.28	−36	−76	−35	Lo > Hi
R Cerebellum	73	19.38	6	−79	−14	Lo > Hi
Source by target probability interaction						
None.						
Overlap of source and target probability effects						
None.						

Notes: Peak F-values and coordinates refer to peak of activated cluster. Number of supra-threshold voxels in cluster (# vox), F value of the main effect (Peak F), coordinates of the peak voxel within the cluster in MNI stereotaxic space (Coords {x, y, z}), direction of the effect (Dir): Perceived > Imagined (P > I); Low target probability > High target probability (Lo > Hi). Gyrus (Gy), Superior Parietal Lobe (SPL), Supramarginal Gyrus (SMG), Left (L), Right (R).

probability on successful retrieval activity. Using this same model we were also able to examine whether there were brain areas where successful retrieval activity co-varied with individual differences in criterion. Activity in both left SPL and bilateral DLPFC co-varied significantly with individual differences in criterion.

We ran a separate second-level ANCOVA model entering individual subject estimates of item memory (d') for each of the source and target probability conditions as regressors. Including estimates of item memory accuracy had very little impact on the whole-brain effects of either source or target probability. Finally, estimates of reaction time (RT) were entered into a separate ANCOVA model, which again, did not influence the effects of either source or target probability on successful retrieval activity.

3.4.2. Source and target probability effects on successful retrieval activity defined by Hits > Misses contrasts

While ‘retrieval success’ effects are most commonly identified by contrasting activity associated with hits and correct rejections, an alternative approach is to compare hit trial activity to activity elicited by ‘misses’ or studied items mistakenly judged to be new. Both approaches have advantages and drawbacks for isolating neural correlates of successful

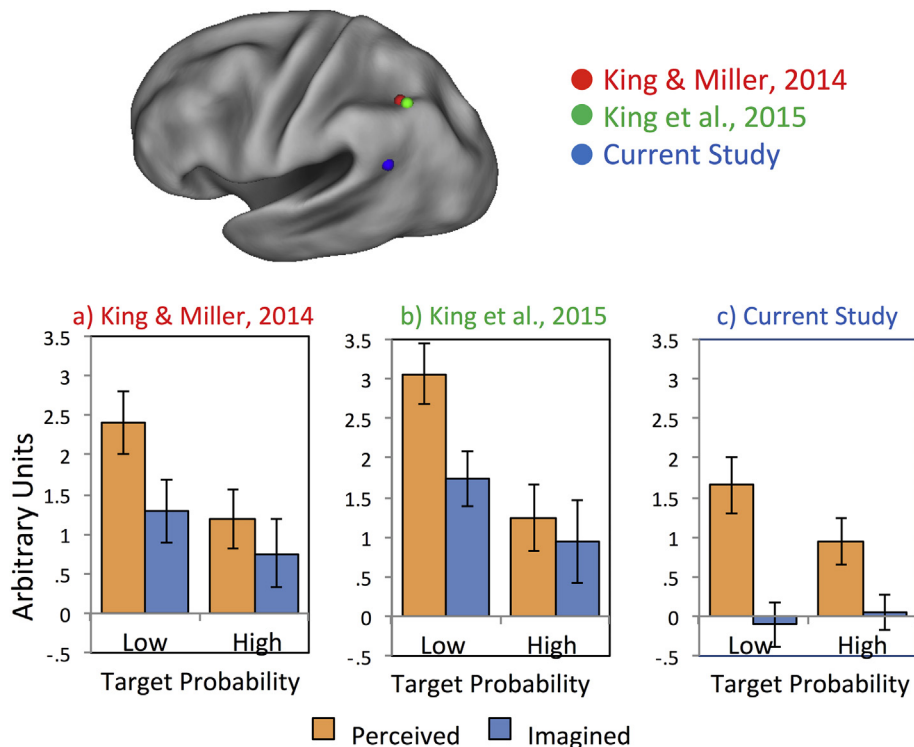


Fig. 5 – Regions of Interest (ROI) Analyses. Regions of interest were constructed as 5 mm spheres centered on the peak of the source effect (Perceive > Imagine) from two prior studies and the current study. ROIs are projected as foci on the inflated surface caret brain (caret5) in red (King & Miller, 2014), green (King et al., 2015), and blue (current study). Average parameter estimates of successful retrieval activity (Hits > CRs) associated with each source/target probability condition are represented as bar graphs and error bars reflect the standard error of the mean. See Results – ROI Analyses for the results of the statistical analyses comparing estimates of retrieval activity within each ROI across source and target probability conditions.

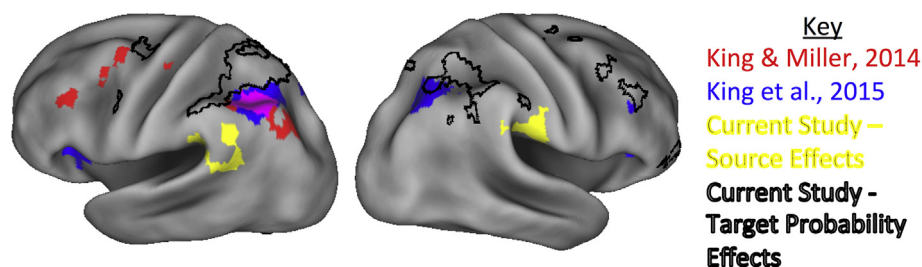


Fig. 6 – Overlap of source effects from current and previous studies. Reported source effects (perceive > imagine) from two previous studies (King & Miller, 2014; King et al., 2015) are projected onto the inflated surface caret brain (caret5) along with source and target probability effects from the current study. Regions that showed greater retrieval phase activity associated with items that were perceived than imagined at encoding in King & Miller, 2014 are depicted in red. Regions that showed greater successful retrieval activity associated with perceived than imagined events in King et al., 2015 are shown in blue. The overlap of regions exhibiting this source effect in both previous studies are shown in magenta. Regions that showed greater successful retrieval activity for perceived than imagined events in the current study are shown in yellow. There was no overlap in voxels exhibiting successful retrieval activity from the current study and either of the two prior studies. Clusters of voxels that exhibited target probability effects (low > high) on successful retrieval activity (Hits > CRs) in the current study are outlined in black.

retrieval. Comparing hits with correct rejections holds constant accuracy of the response (both hits and correct rejections are accurate responses) but not study history (hits are old items whereas correct rejections are new items). In contrast, comparing hits with misses allows item history to be held constant, but is confounded by response accuracy. Here, for the majority of our analyses that involved identifying neural correlates of successful retrieval, we used the more common approach of contrasting hits with correct rejections; however, we also repeated each of the whole-brain analyses contrasting hits with misses instead of correct rejections. The results of these analyses are depicted in Supplementary Figs. 2 and 3. The results were qualitatively similar to the original analyses, only there were fewer voxels, overall, that exhibited a significant effect at the $p < .001$ threshold. For instance, while the perceive/low target probability condition still elicited a robust, widespread LPPC successful retrieval response, the relatively less robust effects that had previously been observed in both the imagine/low probability and perceive/high probability conditions were no longer detectable. Similarly, main effects of source and target probability on successful retrieval activity were no longer significant at the $p < .001$ threshold, but when this threshold was reduced to $p < .005$ (voxel extent = 68), source and target probability effects comparable to those from the original hits > CRs analysis were detected. Using this approach there again was no overlap in regions exhibiting source and target probability effects.

4. Discussion

The current study investigated whether internal/external source effects on LPPC successful retrieval activity can be explained by an inherent tendency to adopt a more conservative response bias when making memory judgments about perceived relative to imagined events. The behavioral results indicated that indeed, subjects were more conservative when making judgments about perceived than imagined events. However, the neuroimaging data did not support the

hypothesis that this difference in response bias could explain source-based differences in LPPC retrieval activity. While there was evidence that both the source and target probability manipulations had a significant effect on the magnitude of parietal retrieval activity, these effects occurred in non-overlapping regions. Target probability influenced activity predominately in SPL, bilaterally, whereas source effects occurred in more ventral regions of LPPC, in SMG and the ventral bank of IPS. Importantly, no voxels exhibited effects of both source and target probability or a significant source by target probability interaction. These findings demonstrate that disparate parietal regions are sensitive to source and response bias, which implies that differences in response bias associated with judgments of perceived and imagined events cannot account for source-based differences in parietal retrieval activity. In the following paragraphs, we discuss how each of the main findings (source and target probability effects on LPPC retrieval activity) relate to prior findings and propose potential mechanistic explanations.

The findings from the current study, in concert with our two prior studies (King & Miller, 2014; King et al., 2015), suggest that while retrieval of memories encoded through perception is associated with a robust parietal successful retrieval response, for memories that were generated through imagination, this response is far less robust or in some instances undetectable. Here, we will refer to evidence for this dissociation as ‘source effects,’ but it is important to note that these source effects differ from the source accuracy effects that are commonly reported in the literature (i.e., greater activity associated with correct than incorrect source attributions), and instead refer to variations in retrieval activity according to internal/external (i.e., perceived/imagined) source.

Taken together, the results from the current study combined with our two previous studies (King & Miller, 2014; King et al., 2015) have significantly advanced our understanding of the characteristics of source effects in LPPC. For instance, we previously demonstrated that source effects occurred regardless of whether items were attributed to perception or imagination (King & Miller, 2014). In other words, perceived

items that were both accurately attributed to perception and misattributed to imagination elicited a greater response in LPPC than both accurately attributed and misattributed imagined items. Hence, the variance in the parietal response was better explained by the manner in which memories were encoded (perception or imagination) than by any processing mechanism that would lead to a particular source judgment. Here, we found additional evidence that LPPC source effects are driven more by the source of encoded information than by processes associated with making a specific memory judgment. We demonstrated that LPPC source effects occurred not only for perceived/imagined/new source judgments, but also for old/new item recognition discriminations. These findings are compelling because the task in the current study was such that retrieval of source information was not necessary for making accurate old/new discriminations. Hence, we cannot know whether participants were retrieving source details at all, or whether participants were falsely retrieving inaccurate source information. However, given that at test, trials from each source condition were identical with the only exception being that cue words had been paired with either a perceived or imagined picture at encoding, source effects at retrieval must have been a consequence of retrieved mnemonic information. These findings provide compelling evidence that distinct neural mechanisms are involved in the representation and processing of memories derived through perception and imagination even when retrieval of source information is not necessary to meet the demands of the retrieval task. Further, they suggest that source effects more likely reflect the distinct processes involved in representing perceived and imagined memories, as opposed to processes that are associated with a particular task demand or behavioral outcome.

Across the three studies (King & Miller, 2014; King et al., 2015, and current study), LPPC source effects were observed across various deviations in the experimental task and design. For instance, LPPC source effects were observed both when the encoded stimuli were photos and sentences, over both relatively short (~20 min) and long (24 h) retention intervals, and both when encoding was incidental and intentional. LPPC source effects were also consistently observed despite variations in discernable patterns of behavior. For example, they occurred both when item memory performance was better (King & Miller, 2014) and worse (King & Miller, 2014 and current experiment) for perceived than imagined events, when source accuracy performance differed (King & Miller, 2014) and did not differ (King et al., 2015) according to source, and when reaction times were similar (King & Miller, 2014), faster (King et al., 2015), and slower (current study) for perceived relative to imagined events. Combined, these studies demonstrated that LPPC is more active during retrieval of perceived than imagined events regardless of variations in behavioral performance and experimental design.

Understanding the underlying cause for source dissociations on retrieval activity could benefit our understanding of the precise functional mechanisms underlying LPPC contributions to memory retrieval. One plausible explanation for these source effects is that internally generated memories are more conceptual than perceptual, and LPPC may be less involved in integrating or evaluating conceptually-based information. However, we tested this in a previous study by

comparing successful retrieval activity associated with both perceived and imagined pictures and sentences (King et al., 2015). Memories for internally generated images, which were rated as highly vivid, failed to elicit a successful retrieval response, whereas memories for perceived sentences, which contained little perceptual detail, elicited a robust response. This suggests that a difference in the perceptual/conceptual nature of perceptually derived and internally generated memories cannot explain differences in LPPC activity. Another possibility is that while LPPC acts as a convergence zone for mnemonic inputs and cognitive processes when the mnemonic information is perceptually derived, another brain region facilitates this convergence when the mnemonic information was generated internally. We have yet to identify a brain region that is consistently more active during retrieval of internally generated than externally derived memories; however, this may be due to limitations in our experimental design or measurement precision. Alternatively, if LPPC successful retrieval activity reflects the integration of multisensory information, it is possible that internally generated memories require less integration than perceptually derived memories, if they are stored as more cohesive, unitized representations. Future work will be necessary to determine the underlying cause of source effects in LPPC, but given the ubiquity of successful retrieval effects in the literature, understanding why internally generated memories fail to elicit the robust parietal response that is commonly observed in association with retrieval of externally derived memories should provide valuable insight into the mechanistic contributions of LPPC to memory retrieval.

It is important to note that there were some regional dissociations between the LPPC areas that exhibited source effects in our current and prior studies (King & Miller, 2014; King et al., 2015). For instance, although source effects were detected in a small portion of the IPS in the current study, this activation was not as widespread as in previous studies, where activation extended dorsally toward SPL and posteriorly toward angular gyrus (King & Miller, 2014; King et al., 2015). And unlike in previous studies, source effects in the current study occurred more ventrally and anteriorly, encompassing much of the SMG. To understand these different patterns of activity it is important to consider the experimental variables that differed across studies. The main feature distinguishing the current from previous studies was the nature of the retrieval task. Here, participants made old/new recognition judgments, whereas in previous studies, they made perceived/imagined/new source judgments. As was previously discussed, while the old/new task did likely elicit retrieval of source details on a subset of trials, either automatically or intentionally to inform the old/new decision, this probably occurred less frequently than when the task was a source discrimination and accurate judgments required reactivation or source information. Hence, the relative reduction in IPS effects in the current study can be explained by a diminished demand to retrieve source details in the old/new recognition task. Consistent with this notion, studies have demonstrated that IPS is more active during source compared to item memory judgments (Dobbins & Wagner, 2005; Dobbins, Foley, Schacter, & Wagner, 2002; Fan, Gay Snodgrass, & Bilder, 2003; Han, O'Connor, Eslick, & Dobbins, 2012). These findings have been interpreted as

evidence that IPS is involved in representing contextual details associated with episodic memories. Our results qualify this notion, suggesting that IPS is specifically involved in representing perceptually derived, but not internally generated contextual details of memories.

It is less apparent why ventral anterior regions of LPPC showed source effects in the current study and not in previous studies. One possibility is that this activity reflects the bottom-up capture of attention by stored mnemonic information. Findings from a number of studies suggest that activity in ventral anterior regions of LPPC may reflect the reflexive capture of attention that occurs when there is a strong match between a retrieval cue and stored mnemonic representations (e.g., Ciaramelli, Grady, & Moscovitch, 2008; Hutchinson, Uncapher, & Wagner, 2009; Hutchinson et al., 2009). It is possible that retrieving perceptually derived contextual details captures bottom-up attention to a greater extent during item memory versus source memory discriminations, as retrieval of any contextual information is sufficient to make the former, but not the latter judgment. Future studies involving the direct, within-subjects comparison of brain activity associated with old/new item memory and internal/external source judgments will be necessary to determine whether retrieval of perceived events reliably activates ventral anterior LPPC more during item than source memory judgments.

In addition to the findings of a main effect of source on LPPC activity, the current study also replicated previous findings demonstrating that dorsal LPPC retrieval activity varied as a function of the probability (true or perceived) that a given test item was old (Aminoff et al., 2015; Jaeger et al., 2013; O'Connor et al., 2010; Vilberg & Rugg, 2009). Several hypotheses have been proposed to account for this effect. One proposal is that differences in activity as a function of target probability may reflect variations in the saliency of retrieval cues (Vilberg & Rugg, 2009). In retrieval blocks where old trials occur infrequently, cues that elicit a familiarity response are more salient than when old trials occur more regularly, and this difference in saliency may be driving differences in parietal activity. A related explanation suggests that probability effects are due to an unexpected familiarity response, as in low target probability conditions, the relatively infrequent old trials violate the probability, and therefore the expectancy, that the item should be new (Jaeger et al., 2013; O'Connor et al., 2010). Another possibility is that adopting a conservative response bias, which is common in low target probability conditions, activates dorsal parietal regions involved in cognitive control because under these conditions retrieval evidence is monitored more stringently before an item is endorsed as old (Aminoff et al., 2015). A distinguishing feature between these hypotheses relates to the prediction of an interaction between target probability and memory strength on parietal activity. According to both the saliency and unexpected familiarity hypotheses there should be an interaction between target probability and memory strength, as in both cases, the response depends on the ability to distinguish between old and new items. In other words, in low target probability conditions, the magnitude of the saliency or unexpected familiarity response should increase as a function of increasing familiarity. Indeed, Jager et al. found evidence for a

relationship between d' and the unexpected familiarity response in parietal cortex. However, Aminoff and colleagues demonstrated that differences in response bias could account for variance in parietal activity above and beyond any variance accounted for by differences in d' , lending support for the response bias hypothesis. Here, we found additional support for the response bias hypothesis, as we failed to identify a significant relationship between d' and parietal retrieval activity. In addition, including d' as a covariate in the regression model did not influence the magnitude or extent of target probability effects. While the current study was not specifically designed to address which of these hypotheses can best explain target probability effects, the results suggest that target probability effects are more likely due to a tendency to be more cautious when making old responses in low target probability conditions than to the degree to which old items elicit a saliency or expectancy violation response.

While target probability effects have been consistently reported in dorsal regions of LPPC, in SPL, they have been observed less consistently in IPS. Aminoff et al. (2015) suggested that the inconsistency of IPS effects could be due to differential patterns of behavior across studies. As mentioned in the introduction, whether or not target probability manipulations influence response bias depends on a number of factors, including whether participants were aware of the probability manipulation. It appears that IPS target probability effects occur only when response bias varies concurrently with target probability (Aminoff et al., 2015; Jaeger et al., 2013). Hence, target probability effects in IPS are thought to occur when participants adopt a more conservative response bias in low than high probability conditions. However, in the current study, while response bias did vary across target probability conditions, we failed to identify an effect of target probability on IPS activity. One possible explanation for this discrepancy in findings is that in our study, target probability did not influence behavior enough to elicit an associated effect in IPS. In comparison to Aminoff et al., criterion in the current study was similarly conservative in the low target probability condition ($c(\text{Aminoff}) = .30/.28$; $c(\text{current}) = .47/.33$); however, criterion in the high target probability condition was not as liberal in our study compared to in Aminoff et al. ($c(\text{Aminoff}) = -.32/-.31$; $c(\text{current}) = .04/-.16$). It is possible that if our target probability manipulation had caused a more pronounced behavioral effect then we would have observed a probability-based difference in IPS activity.

The main finding of the current study was that there was no overlap in the LPPC regions that showed source and target probability effects. Similarly, when we compared source and target probability effects from the current study to source effects observed in our two previous studies (King & Miller, 2014; King et al., 2015) using statistically thresholded overlap maps we again found no evidence for an overlap in the left LPPC regions that exhibited target probability and source effects. However, the results of the ROI analysis did suggest some degree of overlap between source and target probability effects. Specifically, the LPPC region that showed the peak source effect in a prior study (King et al., 2015) also demonstrated a main effect of target probability on retrieval activity in the current study. This finding, along with the finding that

source effects in the current study occurred in different LPPC regions than in previous studies can be interpreted in several ways. First, it is possible that the source effects across the three studies reflect the same underlying mechanism, but this mechanism is spatially imprecise. If this is the case, then it is possible that under different experimental circumstances source effects may be observed in the same dorsal LPPC regions that exhibit target probability effects. Another possibility is that the findings across studies reveal three functionally distinct regions: one region that exhibited source effects when the task was a perceived/imagined/new judgment, a second region that exhibited source effects when the task was an old/new discrimination, and a third region that exhibited the target probability effect in the current study. With this latter explanation, again, it appears that the first source sensitive region may exhibit target probability effects under some circumstances. Regardless of which of these explanations can better account for the findings, it appears that there may be instances where the same LPPC region exhibits both source and target probability effects. However, given that source effects in the current study were detected in LPPC regions where activity did not vary with the target probability manipulation or with individual differences in response bias, the current findings demonstrate that LPPC source effects cannot be fully accounted for by a difference in the response bias associated with judgments of previously perceived and imagined events.

To summarize, the results of the current study suggest that although individuals tended to be more conservative in their recognition memory judgments of perceived than imagined events, this difference in response bias cannot account for source-based differences in parietal activity. Instead, it appears that distinct subregions of LPPC showed variations in successful retrieval activity depending on source and response bias. Dorsal regions of LPPC, in SPL, showed greater successful retrieval activity when participants adopted a more conservative response bias, suggesting that this region may contribute to the control processes involved in monitoring retrieved information. Alternatively, more ventral regions, including parts of IPS and SMG were more active during retrieval of perceived than imagined events. Importantly, these effects could not be explained by differences in response bias. This suggests that areas of LPPC that are thought to contribute to successful retrieval either through representing contextual details or directing attention toward stored mnemonic information are preferentially involved in supporting retrieval of perceptually derived rather than internally generated memories. These findings have important implications for theories of parietal contributions to memory retrieval, as they demonstrate that parietal activity can be directly associated with the source of mnemonic information rather than the supporting cognitive processes that occur regardless of the nature of retrieved content.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.04.002>.

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