The Neural Basis of Recollection Rejection: Increases in Hippocampal–Prefrontal Connectivity in the Absence of a Shared Recall-to-Reject and Target Recollection Network

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Abstract

■ Recollection rejection or "recall-to-reject" is a mechanism that has been posited to help maintain accurate memory by preventing the occurrence of false memories. Recollection rejection occurs when the presentation of a new item during recognition triggers recall of an associated target, a mismatch in features between the new and old items is registered, and the lure is correctly rejected. Critically, this characterization of recollection rejection involves a recall signal that is conceptually similar to recollection as elicited by a target. However, previous neuroimaging studies have not evaluated the extent to which recollection rejection and target recollection rely on a common neural signal but have instead focused on recollection rejection as a postretrieval monitoring process. This study utilized a false memory paradigm in conjunction with an adapted remember–know–new response paradigm that separated "new" responses based on recollection rejection from those that were based on a lack of familiarity with the item. This procedure allowed for parallel recollection rejection and target recollection contrasts to be computed. Results revealed that, contrary to predictions from theoretical and behavioral literature, there was virtually no evidence of a common retrieval mechanism supporting recollection rejection and target recollection. Instead of the typical target recollection network, recollection rejection recruited a network of lateral prefrontal and bilateral parietal regions that is consistent with the retrieval monitoring network identified in previous neuroimaging studies of recollection rejection. However, a functional connectivity analysis revealed a component of the frontoparietal rejection network that showed increased coupling with the right hippocampus during recollection rejection responses. As such, we demonstrate a possible link between PFC monitoring network and basic retrieval mechanisms within the hippocampus that was not revealed with univariate analyses alone. ■

INTRODUCTION

False recognition is a memory error that occurs when new information is misidentified as having been previously encountered (for reviews, see Dennis, Bowman, & Turney, 2015; Arndt, 2012; Schacter, 1999). As such, the ability to suppress or avoid false recognitions—and instead correctly reject novel information—is critical to maintaining accurate memory. Although a number of mechanisms have been posited to support the correct rejection of new information presented during retrieval (i.e., lures), one process in particular—known as "recall-to-reject" or recollection rejection—is considered to be particularly critical for rejecting retrieval lures that share features with targets. Recollection rejection occurs when the presentation of a retrieval lure triggers the recall of a target item, thereby allowing for the detection of mismatch between target and lure features (Kumaran & Maguire, 2007a, 2007b; Brainerd, Reyna, & Estrada, 2006; Brainerd, Reyna, Wright, & Mojardin, 2003; Brainerd

& Reyna, 2002). Accordingly, as both recollection rejection and target recollection are posited to involve the retrieval of specific features of a previous event, it follows that these two memory responses share a common recollection-based memory signal. Although the correspondence between the retrieval mechanism supporting recollection rejection and target recollection has been posited in the theoretical literature (Brainerd et al., 2003) and demonstrated in the behavioral literature (Matzen, Taylor, & Benjamin, 2011; Brainerd et al., 2006; Lampinen, Watkins, & Odegard, 2006; Jones, 2005; Odegard & Lampinen, 2005; Odegard, Lampinen, & Toglia, 2005; Lampinen, Odegard, & Neuschatz, 2004; Dobbins, Kroll, Yonelinas, & Liu, 1998), it is not known if the two forms of recollection rely on similar neural mechanisms. To address this issue, this study sought to characterize the neural mechanisms supporting both target recollection and recollection rejection in the same individuals and evaluate the extent to which a common recollection signal supports both processes.

Behavioral work has shown that lures sharing features with targets can elicit feelings of familiarity that lead to false

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recognition if not opposed by recollection of specific target details (Öztekin, Güngör, & Badre, 2012). Conversely, when familiarity signals in response to lures are weak or absent, this lack of familiarity is sufficient to reject the lure, and recollection processes do not need to be engaged. Thus, correct rejections can be based on either recollection rejection or an absence of familiarity with the lure, but only recollection rejection involves reinstatement of target details. Indeed, studies have shown that the same manipulations that affect target recollection also affect recollection rejection, including imposing response deadlines (Odegard, Koen, & Gama, 2008; Jones, 2005) and dividing attention during study (Odegard et al., 2008; Odegard & Lampinen, 2005). Behavioral studies thus provide evidence for the role of target recollection in lure rejection.

Despite the correspondence between recollection rejection and target recollection that has been posited by memory theory and behavioral literature, neuroimaging studies of this rejection mechanism have characterized recollection rejection primarily as a postretrieval monitoring process without identifying a clear signal corresponding to the recollection of the target itself (Gallo, McDonough, & Scimeca, 2010; Gallo, Kensinger, & Schacter, 2006; Achim & Lepage, 2005; Lepage, Brodeur, & Bourgouin, 2003). These monitoring processes contribute to false memory suppression by evaluating if the retrieved study information provides sufficient evidence to reject the lure (Gallo, 2004). Specifically, such neuroimaging studies have identified neural regions that contribute to successfully rejecting lures that are associated with feelings of familiarity as a measure of recollection rejection processes (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003). In accord with previous studies investigating retrieval monitoring (Hayama & Rugg, 2009; Bunge, Burrows, & Wagner, 2004; Dobbins, Rice, Wagner, & Schacter, 2003; Zhang, Leung, & Johnson, 2003; Henson, Rugg, Shallice, & Dolan, 2000), such neuroimaging studies have identified a prefrontal network (emphasizing DLPFC) that supports recollection rejection. The notion that these monitoring signals occur postretrieval is supported by ERP studies showing relatively late frontal components that distinguish between old and new items (Ally & Budson, 2007; Wilding & Rugg, 1996). However, neither fMRI nor ERP studies have specifically isolated conscious recollection rejection to determine its degree of overlap with the target recollection network that would be expected to support the recall of target features.

Target recollection occurs when the presentation of an old item elicits retrieval of details from the item's study episode (Tulving, 1985). This reconstruction of a past event is supported by activation within the medial-temporal lobes (MTLs), specifically the hippocampus, and medial prefrontal and parietal regions (for meta-analyses, see Kim, 2013; Spaniol et al., 2009; Ciaramelli, Grady, & Moscovitch, 2008). Specifically, the hippocampus is posited to reinstate patterns of cortical activity that represented the original encoding event (Norman & O'Reilly, 2003; Alvarez & Squire, 1994; Damasio, 1989), whereas midline prefrontal and parietal regions support attention to internal states and self-referential processing associated with retrieving and evaluating episodic memories (Kim, 2010; Buckner, Andrews-Hanna, & Schacter, 2008).

Studies of recollection rejection, however, have not demonstrated neural activity within this canonical recollection network, instead finding that rejection of lures involves the aforementioned prefrontal monitoring network (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003). More specifically, recollection rejection studies have notably failed to identify activation within the hippocampus or any portion of the MTL associated with recollection rejection, which is difficult to reconcile with the MTL's reconstructive role during memory retrieval (Norman & O'Reilly, 2003; Alvarez & Squire, 1994; Damasio, 1989), and the theoretical basis of target recollection underlying recollection rejection in the behavioral literature (Brainerd et al., 2003). In the absence of such a signal, it is unclear by what mechanism target information could be reinstated during recollection rejection. Furthermore, activation within lateral prefrontal monitoring regions has not been directly linked to recall processes in the hippocampus. PFC-mediated monitoring processes are posited to affect decision-making by coordinating with lower-level cognitive processes such as reconstructive retrieval in the hippocampus (Moscovitch, 1992). Although this PFC–hippocampal relationship has been identified with respect to some retrieval operations (Wendelken & Bunge, 2010; Kohler, McIntosh, Moscovitch, & Winocur, 1998), previous studies of recollection rejection have not identified the targets of the prefrontal monitoring regions typically active for this memory response. It is therefore unclear (1) if recollection rejection involves a target recollection signal and (2) if postretrieval processes in PFC are related to the evaluation of those recall signals within the hippocampus.

This disparity between the behavioral and neuroimaging literature in the characterization of recollection rejection may be because of the ways in which recollection rejection has been measured in previous neuroimaging studies. Specifically, recollection rejection has been contrasted with both hits (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003) and other correct rejection responses in a source memory task (Gallo et al., 2010; Gallo, Bell, Beier, & Schacter, 2006). In the former contrast, recollection rejection is defined as neural regions that exhibit greater activation for recollection rejection compared with target recollection, which, because of potential common mechanisms, likely underestimates activity supporting recollection rejection. Thus, it is unclear if the lack of MTL activation identified in previous studies arises because recollection rejection is not hippocampus dependent or because recollection rejection and target recollection recruit the hippocampus to a similar degree. The latter contrast assumes that all correct rejection

responses for a given stimulus type are made based on similar cognitive processes, which conflates the stimulus history with the cognitive mechanism for rejecting the stimulus. Thus, both analysis approaches may not be ideal for identifying common activation supporting both recollection rejection and target recollection.

Target recollection, on the other hand, has typically been identified by comparing recollection hits with familiar hits within the context of the remember–know–new response paradigm that asks participants to distinguish subjectively between recollection-based and familiarity-based retrieval responses (e.g., McDonough, Cervantes, Gray, & Gallo, 2014; Johnson, Suzuki, & Rugg, 2013; Johnson & Rugg, 2007; Fenker, Schott, Richardson-Klavehn, Heinze, & Duzel, 2005; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999). This contrast has the benefit of clearly differentiating recollection processes from target identification based on a general feeling of oldness in the absence of retrieval details of the study event. Thus, to create an analogous contrast for correct rejections, the "new" response within the remember–know–new paradigm needs also to be separated into a recollection-based rejection response and a familiarity-based rejection response. To accomplish this goal, this study used a response paradigm that asked participants to distinguish between "new" responses based on recollection rejection from those that could be rejected without engaging recollection processes. Although previous behavioral studies have utilized this response paradigm to distinguish between strategies for rejecting lures (Meeks, Knight, Brewer, Cook, & Marsh, 2014; Matzen et al., 2011), previous neuroimaging studies have not separated the "new" response in a way that distinguished conscious recollection rejection from other rejection strategies, which is critical to isolating the neural signal associated with recollection rejection. The separation of "new" responses allows for parallel contrasts to be computed for both target recollection and recollection rejection so that recollection rejection is measured similarly to target recollection. Parallel contrasts further provide a means to assess overlap in the neural representations of two recollection responses that are posited to involve a common retrieval signal.

Specifically, this study utilized a false memory paradigm to measure neural processes supporting recollection rejection and separate those processes from rejection strategies that do not involve conscious recollection. To this end, fMRI data were assessed during a retrieval task in which participants were asked to distinguish between recollection- and familiarity-based responses for "old" responses and between recollection-rejection- and unfamiliar rejection-based responses for "new" responses. The goals of this study were the following:

1. To assess the neural basis of recollection rejection by distinguishing between correct rejections of lures based on retrieval of target details from correct rejections of lures that are unfamiliar. It was predicted that this analysis would both replicate previous recollection rejection studies in identifying a monitoring network within lateral PFC and parietal cortex and extend such studies by demonstrating activation within regions typically associated with target recollection (i.e., hippocampus and midline frontal and parietal regions).

2. To test the hypothesis that recollection rejection and target recollection rely on common cognitive and neural mechanisms supporting the reinstatement of encoding details during retrieval. On the basis of memory theory and behavioral evidence, we expected to find common activation throughout the target recollection network. In addition, it was of particular interest to identify a common signal within the MTL supporting the reinstatement of target details and context.

3. To identify differences that may exist between target recollection and recollection rejection. Given the presentation history associated with a target (and the absence of that history with respect to lures), we predicted that target recollection would exhibit stronger activation within the target recollection network. Furthermore, given the high monitoring demands of rejecting related lures, it was predicted that recollection rejection would show greater activity in lateral prefrontal regions compared with target recollection.

4. To use functional connectivity to characterize the relationship between retrieval monitoring processes within prefrontal and parietal regions and retrieval signals within the hippocampus during recollection rejection. It was predicted that monitoring processes associated with recollection rejection would operate in conjunction with reconstructive processes mediated by the hippocampus. Thus, we expected that recollection rejection would show increased functional coupling between components of the fronto-parietal monitoring network and the hippocampus when compared with other rejection responses.

METHODS

Participants

Twenty-seven participants completed the study for monetary compensation. Data from nine participants were excluded from imaging analyses because of failure to complete the task (one participant), insufficient trials in a regressor of interest (seven participants), and movement in excess of 3 mm within a run (one participant), leaving data from 18 participants presented in all analyses (12 women, mean age = 22.3 years, SD = 3.04 years, range = 18–28 years). All participants were right-handed, native English speakers. All participants were screened for contraindications for fMRI, health issues affecting

Figure 1. Stimulus presentation. During study, participants saw images and made a size judgment about the object in the image. During retrieval, participants saw targets, related lures, and unrelated lures and made memory decisions using the adapted remember–know–new paradigm.
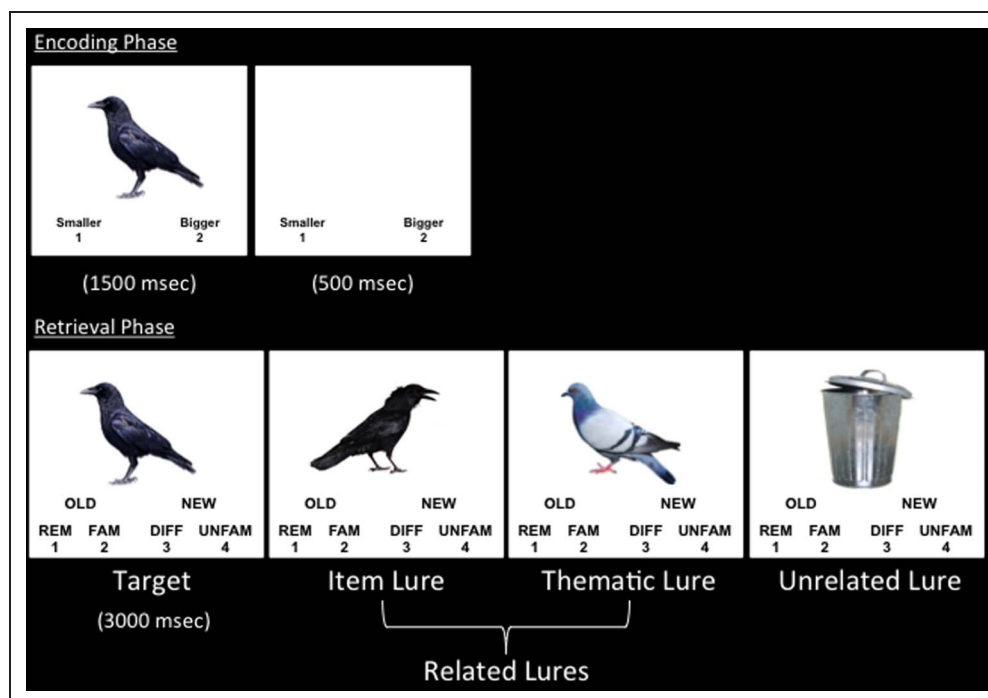
blood flow, previous brain trauma, and medications that are known to affect neural functioning. All procedures were approved by Penn State's Office for Research Protections.

Materials

Stimuli consisted of 316 images of common objects collected from the Band of Standardized Stimuli database (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) as well as an Internet image search. Images were cropped and resized to an approximate size of 400×400 pixels and equated for resolution. Images were displayed at a screen resolution of 1024 (H) $\times$ 768 (V) at 75 Hz. At the viewing distance of 143 cm, the display area was $20°$ (H) $°$ $16°$ (V) with experimental stimuli subtending $5°$ (H) $\times$ $4°$ (V).

Encoding items included 96 images, each an exemplar from a distinct category or conceptual theme. This was to ensure that there was a single target to recall for each lure presented during retrieval. For example, as long as only one bird was presented during encoding, recalling the features of the bird would allow participants to reject a similar yet distinct lure bird shown at retrieval. This distinctiveness has been shown to be an important factor in eliciting the recall-to-reject strategy (Lampinen et al., 2006; Gallo, 2004). However, because the participants were not informed of the distribution of categories across study and test, there was some degree of uncertainty as to the adequacy of recalling the target for rejecting the lure. At retrieval, four types of items were presented: targets, item lures, thematic lures, and unrelated lures (see

Figure 1 for examples). Item lures were an alternative exemplar of the same item presented at encoding. For example, if a crow were presented during encoding, a different crow would be an item lure. Thematic lures were a new item within the same general category or theme of an item presented at encoding. In the above example, a pigeon would be a thematic lure as it is also a bird but is not the same type of exemplar presented during encoding. For power purposes, these two types of related lures were collapsed for neuroimaging analyses. Unrelated lures were items drawn from categories not presented during encoding. A norming study was conducted (15 participants rated related lures; 30 participants rated unrelated lures) to verify that related lures were perceived by participants as more similar to targets than were unrelated lures ($t(43) = 17.32, p < .001$).

Procedure

Participants completed the encoding and retrieval phases in a single scanning session. Encoding was incidental, and participants were instructed to make a size judgment about each of 96 items (i.e., "Is this item bigger or smaller than a shoebox?"). Each image was presented for 1500 msec followed by 500-msec additional responding time before automatically advancing to the next item. Each item was followed by a variable intertrial fixation ($M = 2470$ msec, $SD = 1760$ msec). Images were displayed by COGENT in MATLAB (MathWorks, Natick, MA) and were back-projected onto a screen that participants viewed through a mirror attached to the head coil. Behavioral responses were recorded using a four-button

response box. Scanner noise was reduced with head-phones, and cushioning was used to reduce head motion. The encoding results will be presented in a future paper.

After the encoding phase, participants underwent structural scans before beginning the retrieval task. After the structural scans, participants were given instructions for retrieval and completed several practice trials. Altogether, there were approximately 10 min in between the end of the encoding phase and the beginning of the retrieval phase. During retrieval, participants completed four runs of the task, each lasting approximately 7 min. Participants were presented with all 96 studied items (targets), both the item and thematic lures from each of the encoding categories (96 of each), and 28 unrelated lures. All stimulus categories were presented in an intermixed fashion during each run, pseudorandomly ordered to ensure that no more than three stimuli of the same type were presented sequentially. Each stimulus was displayed for 3 sec while participants made their memory responses. Each trial was followed by a variable intertrial interval ($M =$ 2340 msec, $SD =$ 1440 msec) to aid in deconvolving the hemodynamic response (Dale, 1999). In accord with typical instructions for the remember–know–new paradigm, participants were asked to respond "remember" if they believed that the item was presented during the first phase of the experiment and they remembered specific, vivid details of its prior presentation. Participants were instructed to respond "familiar" if they believed the item was presented during the first phase but they could not recall specific details about its prior presentation. However, instead of the typical "new" response, participants were asked to respond with two distinct "new" options— "unfamiliar" or "different" (Matzen et al., 2011). Participants were instructed to respond "different" if they believed the item was new and they could recall aspects of truly presented item(s) that indicated the item was not presented during the study phase (i.e., a correction rejection based on recollection rejection). They were instructed to respond "unfamiliar" if they believed an item was new because it did not resemble or bring to mind anything from the previous encoding phase (i.e., an unfamiliar correct rejection). A practice session before the retrieval scans ensured that participants understood the retrieval instructions and the distinction between each response option. After completing the retrieval task, participants completed a debriefing questionnaire that asked about their strategies during the task.

fMRI Data Acquisition

Images were acquired using a Siemens (Berlin, Germany) 3-T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was acquired to locate the AC–PC. Images were then prescribed at an oblique angle that prevented data collection in the area of the orbits. A high-resolution anatomical image was acquired in the sagittal plane using an magnetization prepared rapid gradient-echo sequence with a 1650-msec repetition time, 2.03-msec echo time, 256-mm field of view, 256-mm^2 matrix, 160 sagittal slices, and 1-mm slice thickness for each participant. Echoplanar functional images were acquired using a descending acquisition, 2500-msec repetition time, 25-msec echo time, 240-mm field of view, an 80-mm^2 matrix, and 42 axial slices with 3-mm slice thickness, resulting in 3-mm isotropic voxels. Ninety-one volumes were collected in each of two functional runs of the encoding task. One hundred seventy-five volumes were collected in each of four functional runs of the retrieval task.

Image Processing and Analysis

Functional data were preprocessed and analyzed with SPM8 (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm). Images were first checked for movement and scanner artifacts using a time series diagnostic function *TSDiffAana* (Freiburg Brain Imaging, Freiburg, Germany) in MATLAB (MathWorks). Data were then spatially realigned to correct for motion artifacts. The mean functional image across runs was coregistered to the high-resolution anatomical image for each participant, and segmentation was performed. The transformation from these steps was used to spatially normalize the functional images to a standard stereotaxic space using the Montreal Neurological Institute template. Finally, the volumes were spatially smoothed using a 6-mm isotropic Gaussian kernel.

Trial-related activity was modeled in the general linear model with a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function. SPMs for each participant were identified by applying linear contrasts to the beta weights for the events of interest. Regressors were defined by crossing response options (remember, know, different, unfamiliar) with stimuli types (target, related lure, unrelated lure). For targets, individual regressors were defined for "remember" (target recollection) and "know" (target familiarity), whereas "different" and "unfamiliar" responses were collapsed into a single regressor (misses) to increase power. For related lures, individual regressors were defined for "different" (recollection rejection) and "unfamiliar" (unfamiliar rejection) responses, whereas "remember" and "know" responses were collapsed into a single regressor (related false alarms) to increase power. Finally, for unrelated lures, a single regressor was created for "unfamiliar" responses, whereas all other responses were collapsed with no responses and treated as a regressor of no interest. In addition, six regressors corresponding to six motion parameters were included as regressors of no interest.

As an initial assessment of a common recollection signal for hits and correct rejections, a repeated-measures ANOVA was computed within the full factorial module of SPM. Response basis (recollection based, familiarity based) and Trial type (hit, correct rejection) were entered as factors (with their respective levels). Thus, the four regressors

(with their trial count mean and range) included were target recollection ($M = 51.1$, range = 29–72), target familiarity ($M = 25$, range = 11–41), recollection rejection ($M = 83.9$, range = 41–125), and unfamiliar rejection ($M = 72.6$, range = 34–103). F contrasts were computed to examine main effects of response and trial type with a particular interest in a main effect of response (i.e., common recollection-based signal for hits and correct rejections). The interaction effect was also used to identify other possible neural responses underlying recollection rejection such as regions whose response pattern was similar for recollection rejection and target familiarity, indicating a potential neural substrate of familiarity associated with related lures even if they are also associated with a recollection signal. Post hoc t tests were computed within SPM to investigate the nature of any significant F effects.

To identify neural networks supporting target recollection and recollection rejection, t contrasts were computed. Neural activity corresponding to target recollection was defined by comparing "remember" and "know" responses to targets. Neural activity corresponding to recollection rejection was defined by comparing "different" and "unfamiliar" responses to related lures. To confirm results from the above-described main effect of response basis (i.e., investigating similar neural activity for target recollection and recollection rejection), a conjunction analysis was performed within SPM (Nichols, Brett, Andersson, Wager, & Poline, 2005). To identify differences associated with target recollection and recollection rejection, direct comparisons between the two recollection-based responses were computed and inclusively masked with the appropriate contrast to take familiarity-based responding into account. For example, target recollection was contrasted with recollection rejection within an inclusive mask of the contrast Target recollection > Target familiarity. Similarly, recollection rejection was contrasted with target recollection within an inclusive mask of the contrast Recollection rejection > Unfamiliar rejection.

To identify functional connectivity between postretrieval monitoring regions in PFC and parietal cortex and MTL-based retrieval processes, generalized psychophysiological interactions were used (McLaren, Ries, Xu, & Johnson, 2012). On the basis of previous research linking lateral PFC and parietal cortex to monitoring and attentional processes during retrieval (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Henson et al., 1999), three seed regions were chosen by identifying portions of PFC and parietal cortex showing the strongest recollection rejection effect (i.e., peak from the Recollection rejection > Unfamiliar rejection contrast). Two peaks were identified from PFC, corresponding to one seed from each hemisphere. This included portions of right inferior frontal gyrus (IFG; Talairach and Tournoux [T&T] coordinates: [48, 32, 16]) and left middle frontal gyrus (MFG; T&T coordinates: [−48, 24, 36]). One peak was identified from parietal cortex as one cluster spanned both hemispheres (right angular gyrus; T&T coordinates: [36, −63, 51]). The generalized psychophysiological

interaction model was created by adding task regressors (defined above) to a design matrix also including the deconvolved time course from each seed region and their interactions with the recollection rejection and unfamiliar rejection regressors. The model was estimated in each participant with t contrasts between recollection rejection and unfamiliar rejection also computed. One-sample t tests were used to compute group-level contrasts. Given a priori predictions about the increased demand on retrieval monitoring during recollection rejection as compared with unfamiliar rejection, results of the functional connectivity analysis were investigated within an anatomical mask of the MTL as defined by the Wake Forest University AAL Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003).

To determine a cluster threshold corrected for multiple comparisons at $p < .05$, Monte Carlo simulations were used as implemented by 3dclustsim in AFNI (Cox & Hyde, 1997). The input to this simulation was the search space (gray matter mask using the Wake Forest University AAL Pickatlas), smoothness in millimeters ($x, y, z = 11.98$, 11.73, 10.1), and the uncorrected p threshold ($p < .001$), resulting in a voxel extent of 30 required to correct for multiple comparisons at $p < .05$. An additional simulation was run to determine a correction specific to the MTL (bilateral hippocampus and parahippocampal gyrus) to allow for ROI analyses in this critical memory region. Within this MTL mask, an uncorrected threshold of $p < .001$ and an extent threshold of 3 voxels resulted in a corrected threshold of $p < .05$.

RESULTS

Behavioral

A one-way, repeated-measures ANOVA was computed using "different" responses to targets, related lures, and unrelated lures to test the hypothesis that related lures are more likely to elicit a recollection rejection process than unrelated lures or targets. Results revealed a significant effect of Trial type ($F(1.48, 25.14) = 109.39, p < .001$, with a Greenhouse–Geisser correction). Bonferroni-corrected pairwise comparisons revealed that, consistent with predictions, related lures were associated with significantly higher recollection rejection rates when compared with both targets ($t(16) = 8.52, p < .001$) and unrelated lures ($t(16) = 12.86, p < .001$). In addition, targets were associated with a significantly higher recollection rejection rate than unrelated lures ($t(16) = 4.89, p < .001$; see Table 1 for means and standard deviations). To test the hypothesis that unrelated lures—lures that are relatively distinct from targets—are typically rejected based on lack of familiarity, a one-way, repeated-measures ANOVA was computed on "unfamiliar" responses to targets, related lures, and unrelated lures. Results revealed a significant effect of Trial type ($F(2, 32) = 693.25, p < .001$) with post hoc tests indicating that unrelated lures were associated with the highest rates of "unfamiliar" responses, significantly

Table 1. Behavioral Response Rates and RTs

	Rate, M (SD)	RT, M (SD)
Target		
Remember	0.53 (0.12)	1354 (177)
Familiar	0.26 (0.10)	1854 (212)
Different	0.14 (0.07)	1796 (216)
Unfamiliar	0.05 (0.03)	1782 (435)
Related lure		
Remember	0.05 (0.02)	1513 (418)
Familiar	0.14 (0.12)	1943 (332)
Different	0.43 (0.13)	1744 (233)
Unfamiliar	0.38 (0.11)	1641 (197)
Unrelated lure		
Remember	0.002 (0.008)	1889[a]
Familiar	0.02 (0.03)	1967 (561)
Different	0.05 (0.05)	1632 (386)
Unfamiliar	0.92 (0.07)	1392 (184)

[a]No SD is reported as only one participant had even a single "remember" response to an unrelated lure.

greater than either targets ($t(16) = 52.86$, $p < .001$) or related lures ($t(16) = 19.39$, $p < .001$). In addition, the proportion of "unfamiliar" responses to related lures was higher than to targets ($t(16) = 13.19$, $p < .001$). Taken together, these results indicate that the degree of similarity between targets and lures affects the likelihood that recollection rejection will be utilized to reject lures.

In addition to assessing behavioral differences in accuracy, an ANOVA was computed to test for differences in RT across recollection-based and familiarity-based responses. A 2 (Trial type: hit, correct rejection) × 2 (Response basis: recollection based, familiarity based) repeated-measures ANOVA revealed a significant main effect of Response ($F(1, 16) = 23.25$, $p < .001$) and a Trial type × Response interaction ($F(1, 16) = 99.93$, $p < .001$). The main effect of Trial type was driven by faster responses for hits ($M = 1597$, $SE = 42.16$) compared with correct rejections ($M = 1676$, $SE = 43.31$). The main effect of Response was driven by faster responses for recollection-based responses ($M = 1512$, $SE = 36.62$) compared with familiarity-based responses ($M = 1763$, $SE = 42.06$). However, these main effects were qualified by a significant interaction, which showed that recollection-based responses were faster than familiarity-based responses for targets ($t(17) = 10.61$, $p < .001$), whereas RTs for recollection-based and familiarity-based responses to lures were only marginally different ($t(17) = 1.85$, $p = .08$).

Neuroimaging

ANOVA

To assess a potential common neural signal for target recollection and recollection rejection, a 2 (Trial type: hit, correct rejection) × 2 (Response basis: recollection based, familiarity based) repeated-measures ANOVA was computed. Results revealed no regions showing a main effect of Trial type or Response, but one region of the parietal cortex showed a Trial type × Response interaction. Specifically, there was an interaction effect in the precuneus (T&T coordinates of peak: $[-6, -63, 46]$, $k = 134$). Post hoc t contrasts computed in SPM revealed that this region showed greater activation for recollection rejection and target familiarity responses compared with both target recollection and unfamiliar rejection. Thus, this analysis provided evidence for a common target familiarity but not common target recollection signal associated with recollection rejection.

Recollection Rejection and Target Recollection Networks

After the ANOVA, contrasts were computed to identify neural activity that supported recollection-based responses for hits and correct rejections. Regions showing greater activation for target recollection as compared with target familiarity included ventromedial PFC, dorsal anterior cingulate, and posterior cingulate. An ROI analysis of the MTL showed bilateral activation primarily within the hippocampus (see Table 2 for complete results). Regions showing greater activation for recollection rejection as compared with unfamiliar rejection included bilateral IFG, MFG, and superior frontal gyrus; bilateral angular gyrus; and bilateral inferior and superior parietal cortices. An ROI analysis of the MTL showed no significant activation in any portion of this region. Furthermore, only one voxel in the MTL showed greater activation for recollection rejection as compared with unfamiliar rejection even at the very liberal threshold of $p < .05$ uncorrected, providing very little evidence for an MTL-based recollection rejection signal (see Table 3 for complete results).

In addition to evaluating the potential overlap in neural activity supporting recollection rejection and target recollection via a main effect of recollection-based responses (see above), a conjunction of the above-described recollection-based t contrasts was performed (i.e., Target recollection > Target familiarity ∩ Recollection rejection > Unfamiliar rejection). In line with the main effect presented above, the conjunction revealed no region demonstrating both a target recollection and recollection rejection effect. Lowering the threshold for each contrast to $p < .01$ revealed only one cluster of activation within occipital cortex (T&T coordinates: $[48, -60, -6]$, $k = 55$). Similar analyses using an inclusive masking procedure revealed the same pattern of results (i.e., no overlap between target recollection and recollection rejection). Taken together,

Table 2. Neural Activity Associated with Target Recollection

Region	BA	H	Coordinates (T&T)			t	k
			x	y	z		
Target recollection > target familiarity							
Ventromedial PFC	11/32	M	6	21	−18	8.18	469
IFG/MFG	11/47	R	27	27	−16	7.42	31
Dorsal anterior cingulate	24/32	M	−3	−2	31	6.15	54
Posterior cingulate	31	M	−12	−34	41	4.97	38
Hippocampus	−	L	−24	−19	−13	4.86	15
	−	R	24	−22	−13	3.83	3
Target recollection > recollection rejection (inclusively masked)							
Ventromedial PFC	11/32	M	6	21	−18	8.18	268
Dorsal anterior cingulate	24/32	M	−3	−2	31	6.15	43

Significant regions of activation associated with target recollection as compared with target familiarity (top) and target recollection as compared with recollection rejection, inclusively masked with target recollection compared with target familiarity (bottom). BA = Brodmann's area; H = hemisphere; *k* = number of voxel in cluster; M = medial; R = right; L = left.

the results do not support the hypothesis that recollection rejection and target recollection are mediated by a common neural network.

Differences in Target Recollection and Recollection Rejection

Although results revealed little evidence for a common neural signal supporting target recollection and recollection rejection, the question of whether the recollection rejection and target recollection showed significant differences from each other remained. To identify regions showing greater activity for target recollection as compared with recollection rejection, a direct comparison of these two responses was computed within an inclusive mask of the contrast Target recollection > Target familiarity. Results were thus limited to regions already having demonstrated the typical target recollection effect (see above). This analysis revealed that the ventromedial PFC and dorsal anterior cingulate not only showed a typical target recollection effect but also showed significantly greater activity for target recollection than recollection rejection. Although hippocampal activation reached significance for target recollection but not for recollection rejection, the difference between target recollection and recollection rejection was not significant.

A similar analysis was performed to identify regions showing recollection-rejection-specific effects by contrasting recollection rejection with target recollection within an inclusive mask of Recollection rejection > Unfamiliar rejection. Results revealed that activation in left OFC, left MFG, and left inferior parietal cortex showed recollection rejection effects that were distinct from both unfamiliar rejection and target recollection.

Connectivity

In addition to identifying univariate activity underlying recollection rejection responses, we tested the hypothesis that signals in frontoparietal regions associated with recollection rejection are related to MTL-based retrieval signals (i.e., postretrieval monitoring) regardless of the overall magnitude of the MTL response. To do so, a functional connectivity analysis was performed using PFC and parietal ROIs identified as critical to recollection rejection processing in univariate analyses. Functional connectivity was computed between each functionally defined ROI and anatomically defined MTL. The strength of MTL connectivity was compared between recollection rejection and unfamiliar rejection trials using *t* contrasts. Results revealed that the right prefrontal seed (located within the IFG) showed connectivity with the right hippocampus (peak = 24, −22, −8; *k* = 16) during recollection rejection that was significantly greater than that associated with unfamiliar rejection. The locus of this hippocampal cluster was in proximity to the hippocampal cluster from the Target recollection > Target familiarity contrast (see Figure 5B) but did not show statistical overlap in a conjunction analysis. Seeds in the left PFC and right parietal cortex did not show significant connectivity with any portion of the MTL.

DISCUSSION

This study sought to characterize the neural basis of recollection rejection and evaluate the hypothesis that

Table 3. Neural Activity Associated with Recollection Rejection

| Region | BA | H | Coordinates (T&T) | | | t | k |
			x	y	z		
Recollection rejection > unfamiliar rejection							
OFC	11/10	L	−42	51	−7	5.46	161
IFG	45/47	L	−53	21	25	7.06	393
	45/47	R	48	32	16	9.23	177
MFG	46/9/8	R	48	32	19	9.03	516
	10/11	R	42	51	−12	4.86	53
	46/9/8	L	−48	24	36	7.85	461
Superior frontal gyrus	8	R	27	8	52	5.66	28
	8	L	−15	22	58	7.42	80
Dorsomedial PFC	6/32	M	−6	22	47	7.1	363
Caudate	−	L	−12	8	12	7.28	58
	−	R	15	3	12	6.67	62
Supramarginal gyrus	40	R	48	−34	41	7.34	45
Inferior parietal cortex	40	R	48	−37	44	8.64	274
	40	L	−36	−51	39	9.02	409
Angular gyrus	39	L	−33	−49	37	8.76	113
	39	R	36	−63	51	10.07	223
Superior parietal cortex	7	L	−36	−59	54	7.31	241
	7	R	33	−63	51	9.7	172
Precuneus	7	M	12	−65	54	8.38	460
Occipital cortex	18	L	−30	−94	1	5.07	65
Cerebellum	−	L	−36	−61	−34	6.95	559
	−	R	42	−67	−31	6.44	496
	−	M	9	−78	−15	5.53	85
Recollection rejection > target recollection (inclusively masked)							
OFC	10/11	L	−45	42	−9	7.91	66
MFG	6/8	L	−30	2	53	11.76	150
	8/9/46	L	−48	21	36	10.55	218
Inferior parietal cortex	40	L	−36	−57	45	11.74	337
Cerebellum	−	R	39	−67	−31	8.69	146
	−	M	9	−75	−18	7.58	58

Significant regions of activation associated with recollection rejection as compared with unfamiliar rejection (top) and recollection rejection as compared with target recollection, inclusively masked with recollection rejection compared with unfamiliar rejection (bottom).

recollection rejection and target recollection are supported by a common retrieval signal. The results of this study largely replicated previous neuroimaging studies showing that recollection rejection is supported by a lateral frontoparietal network and target recollection is supported by activity in bilateral hippocampus and medial prefrontal regions and the posterior cingulate. Contrary to our predictions, there was little evidence to support the hypothesis that recollection rejection is mediated by similar processes as target recollection. Furthermore, results

showed that the two recollection responses differed such that medial prefrontal regions were more strongly engaged in support of target recollection whereas left-lateralized prefrontal regions differentially supported recollection rejection. Interestingly, although no region of the MTL was shown to support recollection rejection in univariate analyses, a functional connectivity analysis revealed that the right inferior PFC, a component of the frontoparietal recollection rejection network, showed increased connectivity with the right hippocampus during recollection rejection as compared with rejection of lures that did not engage recollection. Taken together, results suggest that recollection rejection and target recollection show little evidence of a common retrieval signal and that recollection rejection instead relies strongly on control and monitoring processes that may evaluate the products of relatively weak hippocampal signals.

Neural Differences Based on Rejection Strategy

Given theoretical and behavioral literature that characterizes recollection rejection as a recall process, the first goal of this study was to identify the recollection rejection network using a response paradigm that could isolate the recollection component of recollection rejection. Specifically, we asked participants to subjectively distinguish between correct rejections based on recollection of the study episode from those based on a lack of familiarity with the lure. This comparison mirrored the traditional contrast used to distinguish between recollection and familiarity responses to targets in the remember–know–New paradigm. Results showed recollection-rejection-related increases in neural activity across wide portions of PFC and parietal cortex, including bilateral OFCs; bilateral IFG, MFG, and superior frontal gyrus (encompassing bilateral DLPFC and ventrolateral PFC); precuneus; bilateral inferior and superior parietal cortices; bilateral angular gyri; and right supramarginal gyrus (see Figure 2).

Previous retrieval studies have associated this frontoparietal network with retrieval monitoring processes that serve to evaluate, monitor, and bind together products of retrieval (for a review, see Mitchell & Johnson, 2009). Such top–down monitoring is posited to show increasing engagement with decreasing distinctiveness of memories, which has been operationalized in studies of lure rejection in terms of the perceptual richness of studied items (i.e., photographs as high and words as low perceptual richness; Gallo et al., 2010; Gallo, Kensinger, et al., 2006) as well as by the type of lure presented (related as opposed to unrelated lures; Bowman & Dennis, 2015). However, the frontoparietal network identified within the present analysis was associated with differences in rejection processes within a single stimulus type (i.e., related lures), and thus the observed activity is not driven by differences associated with the presentation history of the stimulus. Furthermore, behavioral results demonstrate that both rejection strategies served as a basis for rejecting related lures. Thus, although related lures are most often rejected based on

Figure 2. Neural activity associated with recollection rejection (top) and target recollection (bottom).
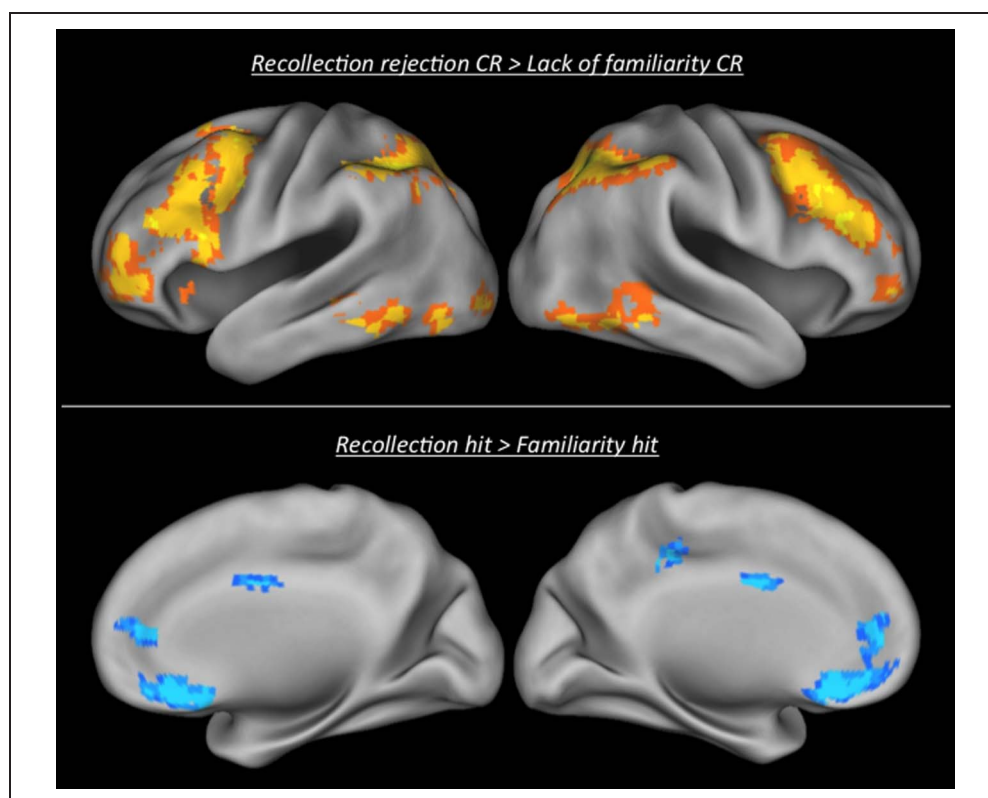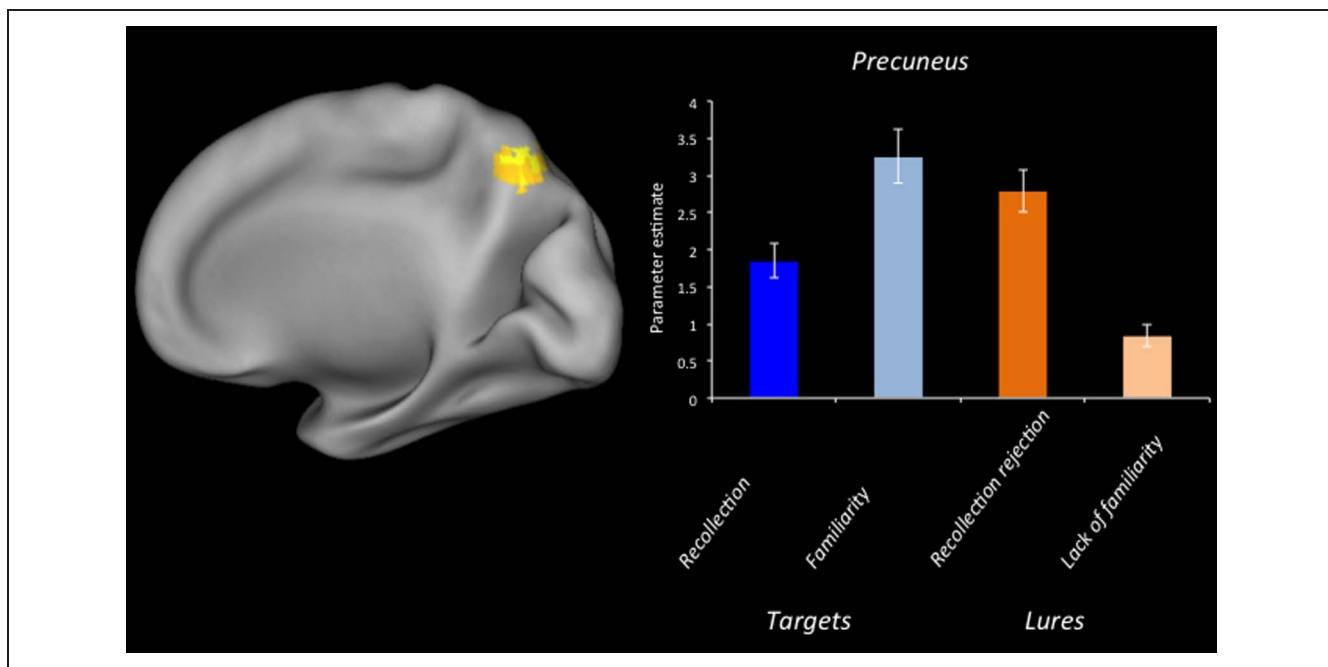
Figure 3. Activity in medial parietal cortex shows an interaction effect in which recollection rejection activity tracks with that of target familiarity.

recollection rejection, a substantial proportion is in fact viewed as sufficiently unfamiliar as to not warrant engaging this strategy. Although the results from the comparison of recollection rejection and rejection without conscious recollection are generally consistent with previous studies (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003), they represent a critical extension given that previous studies did not isolate correct rejections based on retrieval of study details from those that arise because of the absence of familiarity with the lure. By separating these rejection processes within a single stimulus category, this study represents the most direct measure of the neural basis of recollection rejection obtained to date.

Relationship between Recollection Rejection and Target Recollection

Common Activation

The second goal of this study was to evaluate the hypothesis that recollection rejection relies on recollection of a studied item in a manner similar to target recollection. Although the comparison between target recollection and target familiarity revealed activation within bilateral hippocampus, as well as medial prefrontal regions and posterior cingulate cortex, these regions did not overlap with those of the recollection rejection network. Thus, contrary to predictions from the theoretical and behavioral literature, there was no evidence to suggest a common cognitive process linking recollection rejection and target recollection. Importantly, although this was an unexpected result, the separate networks identified for recollection rejection and target recollection were largely consistent with previ-

ous literature (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003). Thus, there is little reason to believe that the lack of overlap was driven by a failure to engage either recollection rejection or target recollection as defined in the behavioral literature. Instead, results suggest that true differences exist in the manner by which recollection processes operate with respect to targets and lures (see Distinct activations section below).

Interestingly, despite the lack of overlap between recollection rejection and target recollection, there was evidence of correspondence between the neural correlates of recollection rejection and target familiarity. Specifically, an interaction effect within the precuneus showed increased activation for these two memory responses compared with both target recollection and unfamiliar rejection (see Figure 3). Consistent with this finding, behavioral false memory studies have shown related lures to be associated with high levels of familiarity because of their similarity to target items (Öztekin et al., 2012; Yonelinas & Jacoby, 1995; Jacoby, 1991) and that such familiarity serves as a signal to engage in further retrieval to recover specific study details that either confirm or disconfirm this feeling (Lampinen, Ryals, & Smith, 2008; Lampinen, Meier, Arnal, & Leding, 2005). Thus, neural activity associated with recollection rejection and target familiarity is consistent with an oldness signal that is not immediately or automatically accompanied by the retrieval of details from encoding.

Distinct Activations

As noted, recollection rejection and target recollection did not show evidence of a common neural basis. However,

direct comparisons between recollection rejection and target recollection were necessary to conclude that the recollection rejection and target recollection networks identified were both nonoverlapping and significantly different from one another. On the basis of hypothesized differences in the strength of the retrieval signals elicited by targets as compared with lures (Rotello, Macmillan, & Reeder, 2004; Hirshman & Master, 1997; Donaldson, 1996), it was expected that recollection rejection would show weaker engagement of regions supporting target recollection. This hypothesis was partially supported by the data as recollection-rejection-related decreases in activation were noted within components of the target recollection network including ventromedial PFC and the dorsal anterior cingulate (although notably absent within the hippocampus and posterior cingulate). Decreases in recollection-rejection-related activation within the target recollection network are consistent with the notion that recollection rejection is associated with a weaker retrieval signal compared with that of target recollection.

As noted above, however, the hippocampal activity associated with target recollection did not differ sig-nificantly from that of recollection rejection. Figure 4 displays mean parameter estimates for both recollection-based and familiarity-based responses within each hippocampal cluster identified in the target recollection contrast. These data demonstrate that the two correct rejection responses lie between the recollection and familiarity responses to targets. For recollection rejection, this intermediate level of activity within the hippocampus may reflect the mixture of familiarity and novelty signals that accompany items that elicit memory for a previous episode but are nonetheless distinct (Kafkas & Montaldi, 2014). Although some theories have suggested that such an instance should maximally recruit the hippocampus or portions thereof (Lacy, Yassa, Stark, Muftuler, & Stark, 2011; Kumaran & Maguire, 2007b), this hypothesis was not supported in this study. One possibility is that such recollection rejection mismatch signals occur only within some portions of the hippocampus (i.e., pattern separation effects identified in CA3/dentate gyrus; Yassa & Stark, 2011) and that the current data average over distinct hippocampal subfields that differentially represent recollection rejection
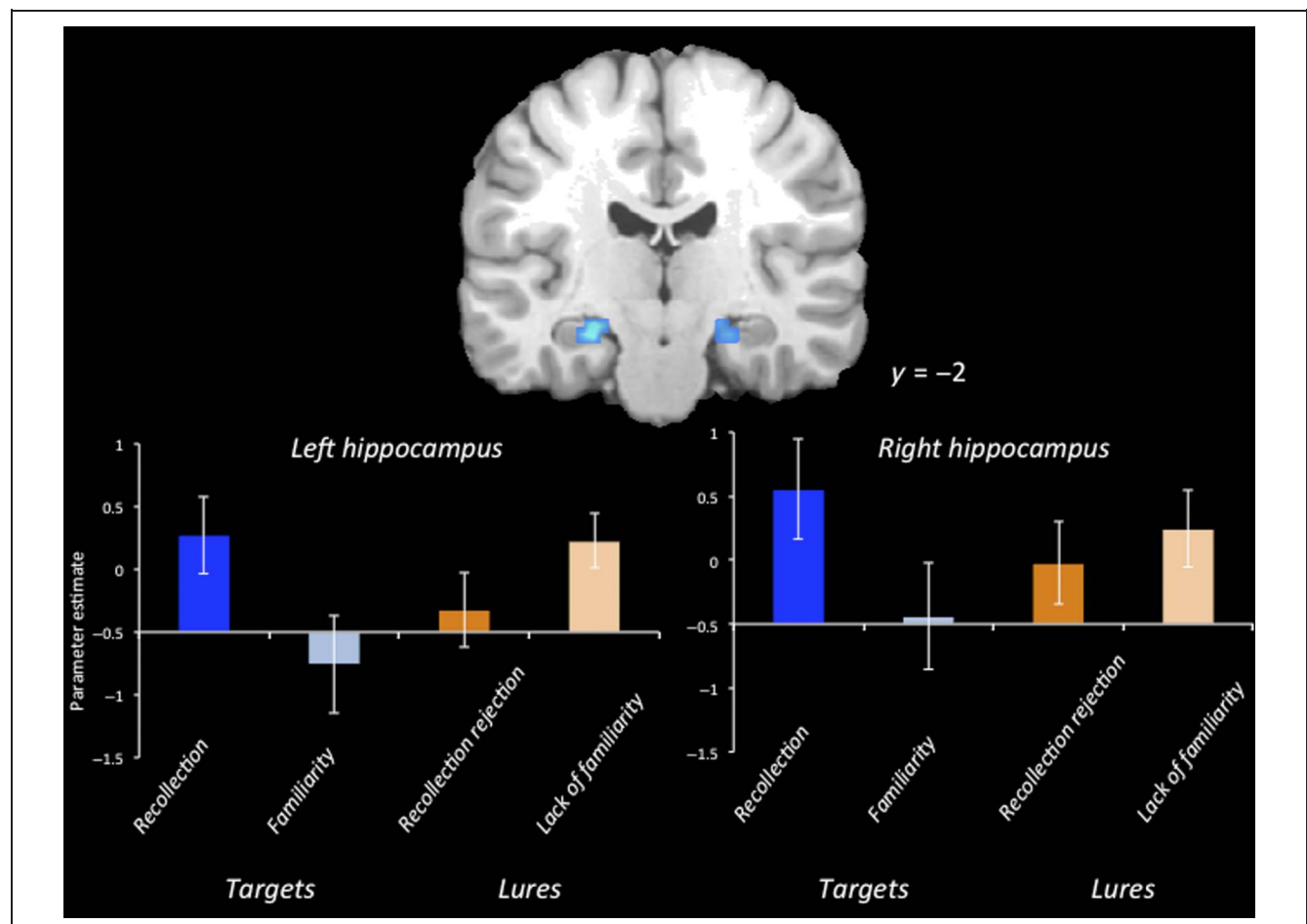

Figure 4. Hippocampal activity associated with target recollection. Parameter estimates for recollection rejection and lack of familiarity responses in this region show that the lack of familiarity response in this region is numerically (but not statistically) greater than that of recollection rejection.

Figure 5. (A) Functional connectivity between right PFC and right hippocampus that is stronger for recollection rejection than unfamiliar rejection. Bar graph depicts average parameter estimates for trial types of interest in the connectivity analysis. (B) Univariate activation from the contrast of True recollection > True familiarity (blue) and hippocampal region showing increased functional connectivity with right PFC (orange) overlaid on the same template to show spatial proximity of the two effects.
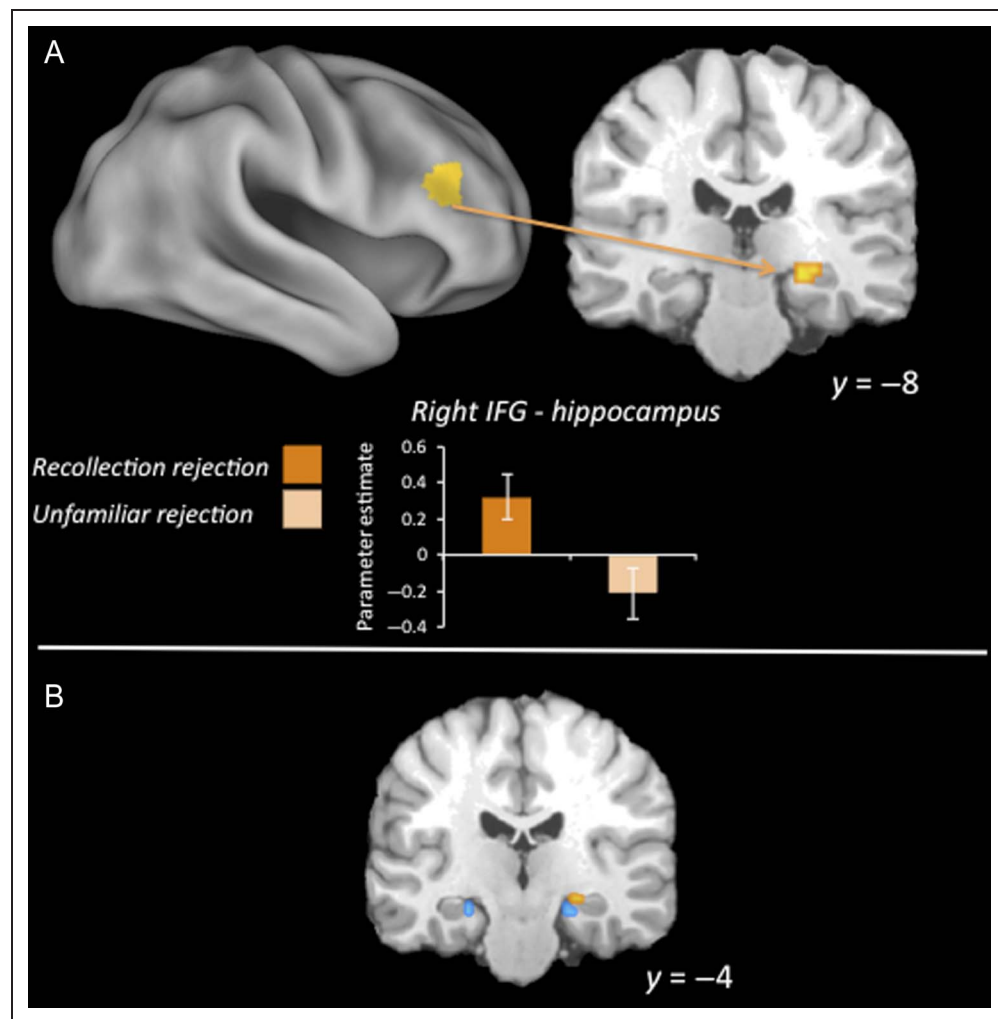
signals. This possibility should be explored in future studies utilizing high-resolution scanning of the MTL to separate these subfields and evaluate recollection rejection responses.

Consistent with hypothesized differences in the need for retrieval monitoring elicited by lures as compared with targets, recollection rejection showed enhanced activation compared with both unfamiliar rejection and target recollection in the left orbitofrontal gyrus, left MFG (including portions of DLPFC), and left inferior parietal cortex. As noted previously, lateral PFC, particularly DLPFC and ventrolateral PFC, has been implicated in strategic processes that operate at particularly high levels in the presence of related lures (Gallo et al., 2010; Gallo, Kensinger, et al., 2006; Achim & Lepage, 2005; Lepage et al., 2003; Okado & Stark, 2003; Schacter et al., 1996). This study extends these findings as it is the first neuroimaging study to ask participants to subjectively distinguish between correct rejection strategies on a trial-by-trial basis. Results thus demonstrated that PFC-mediated monitoring processes are not elicited equally strongly across all related lures but instead by those in which participants consciously engage in a disqualifying strategy.

Recollection-Rejection-Related Functional Connectivity

The final goal of this study was to assess the hypothesis that frontoparietal activation associated with recollection rejection operates in conjunction with the MTL as part of a postretrieval monitoring process that evaluates products of retrieval. Supporting this hypothesis, functional connectivity analyses showed increased connectivity between the right IFG and the right hippocampus during recollection rejection as compared with non-recollection-based rejections (see Figure 5). Functional coupling between the right PFC and hippocampus provides evidence that PFC activity during recollection rejection is related to retrieval processes within the hippocampus, despite that fact that these processes were not detected as part of univariate analyses. This finding is consistent with the notion that PFC monitoring processes are composed of multiple decision-making and control mechanisms that are not specific to memory retrieval but instead operate in multiple cognitive domains (Hayama & Rugg, 2009; Badre & Wagner, 2004). As such, these monitoring responses exert their influence in a particular domain by coordinating with brain regions that support lower-level processing

(Miller & D'Esposito, 2005) such as reconstructive retrieval signals produced in the hippocampus. Critically, although previous neuroimaging studies have identified a prefrontal network that supports recollection rejection, this study is the first to link this network to reconstructive processes within the hippocampus, providing evidence linking the control process with a target memory region. Taken with previously described univariate analyses, this interpretation suggests that the strength of hippocampal signals does not itself lead to a recollection rejection response but rather the strength of monitoring processes attending to such hippocampal signals does. Furthermore, results suggest that monitoring processes may be particularly critical to evaluating weak hippocampal signals elicited by related lures that carry information distinguishing lures from studied items.

Although the above interpretation of PFC activity is consistent with the regions' role in retrieval-related monitoring processes, it is important to note that the present analyses do not provide information about the direction of influence or causality between the right PFC and hippocampus, only that time courses within the two regions are more strongly correlated during recollection rejection responses than "unfamiliar" responses. As such, it is possible that functional coupling between the right PFC and hippocampus instead represents the products of hippocampally based retrieval processes reaching awareness to facilitate decision-making (McIntosh, Rajah, & Lobaugh, 1999, 2003). Under this interpretation, connectivity associated with recollection rejection indicates that retrieved studied information reaches awareness to a greater degree than do responses in which participants reject lures without engaging recollection processes. Overall, these results suggest that the key difference between recollection rejection and other rejection responses to related lures is not necessarily the recall signal per se but the ability of that recall signal to affect decision-making. Future research, however, is needed to differentiate between these top–down and bottom–up explanations.

Conclusions

This study evaluated the neural basis of recollection rejection in relation to both target recollection and non-recollection-based rejection strategies. Contrary to predictions made by memory theory, results demonstrated that recollection rejection was not supported by a target recollection signal and was instead associated with a frontoparietal retrieval monitoring network that was largely distinct from the network supporting target recollection. Although univariate analyses did not show evidence of hippocampal activation associated with recollection rejection, a functional connectivity analysis revealed greater functional coupling between a region of right IFG and right hippocampus during recollection rejection as compared with lure rejection in the absence of recollection. This functional relationship between a region commonly associated with

postretrieval monitoring and a region critical to reconstructive memory processes suggests that postretrieval monitoring during recollection rejection serves to evaluate hippocampal signals that may be only weakly elicited by lures. Thus, recollection rejection does not appear to be associated with a target recollection signal, and rejection of lures based on recollection instead relies on the relationship between PFC control processes and retrieval processes in the hippocampus.

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