Decoding Episodic Retrieval Processes: Frontoparietal and Medial Temporal Lobe Contributions to Free Recall

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Abstract

■ Neuroimaging studies of recognition memory have identified distinct patterns of cortical activity associated with two sets of cognitive processes: Recollective processes supporting retrieval of information specifying a probe item's original source are associated with the posterior hippocampus, ventral posterior parietal cortex, and medial pFC. Familiarity processes supporting the correct identification of previously studied probes (in the absence of a recollective response) are associated with activity in anterior medial temporal lobe (MTL) structures including the perirhinal cortex and anterior hippocampus, in addition to lateral prefrontal and dorsal posterior parietal cortex. Here, we address an open question in the cognitive neuroscientific literature: To what extent are these same neurocognitive processes engaged during an internally directed memory search task like free recall? We recorded fMRI activity while participants performed a series of free recall and source

recognition trials, and we used a combination of univariate and multivariate analysis techniques to compare neural activation profiles across the two tasks. Univariate analyses showed that posterior MTL regions were commonly associated with recollective processes during source recognition and with free recall responses. Prefrontal and posterior parietal regions were commonly associated with familiarity processes and free recall responses, whereas anterior MTL regions were only associated with familiarity processes during recognition. In contrast with the univariate results, free recall activity patterns characterized using multivariate pattern analysis did not reliably match the neural patterns associated with recollective processes. However, these free recall patterns did reliably match patterns associated with familiarity processes, supporting theories of memory in which common cognitive mechanisms support both item recognition and free recall. ■

INTRODUCTION

In recognition tasks, two processes have been posited to support the correct determination that a particular memory probe was previously studied: episodic recollection and item familiarity (Yonelinas, 2002). Episodic recollection provides conscious access to contextual information associated with prior experience; if a probe in a recognition memory task triggers retrieval of contextual information consistent with the target list, the participant can confidently endorse it as studied. In the absence of detailed contextual information, the item may still trigger a sense of familiarity, allowing the participant to correctly identify it as something that was previously encountered. Recently, a number of behavioral studies have implicated both of these processes in free recall (Sadeh, Moran, & Goshen-Gottstein, 2015; Mickes, Seale-Carlisle, & Wixted, 2013; McCabe, Roediger, & Karpicke, 2010), demonstrating that whereas some free recall responses are accompanied by specific contextual details, other responses lack this detail, but the participant still knows that the reported item is from the target list. Although a great many neuroimaging studies have examined the neural circuitry associated with each of these processes

in recognition tasks (e.g., Johnson, McDuff, Rugg, & Norman, 2009; Kahn, Davachi, & Wagner, 2004), only a handful of studies have characterized the neural circuitry engaged during free recall (Kragel, Morton, & Polyn, 2015; Kragel & Polyn, 2015; Shapira-Lichter, Oren, Jacob, Gruberger, & Hendler, 2013; Shapira-Lichter et al., 2012; Long, Öztekin, & Badre, 2010). None of these have directly contrasted neural engagement between recall and recognition tasks. As such, there is a gap in our understanding of the neural basis of human memory: To what extent are the same neural processes engaged during recognition and free recall?

A large number of neuroimaging studies have used event-related fMRI to understand the mechanisms supporting episodic retrieval in the presence of a salient memory probe (for reviews, see Mitchell & Johnson, 2009; Spaniol et al., 2009; Vilberg & Rugg, 2008; Skinner & Fernandes, 2007). In these studies, researchers have developed a number of standard contrasts to disentangle the neural signatures of different cognitive processes during recognition memory tasks (for a review, see Diana, Yonelinas, & Ranganath, 2007). In recognition experiments where the participant is explicitly asked to remember some source characteristic of a probe item, recollective processes have been identified by contrasting neural activity on trials where source was correctly recalled

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(often called Source Hits) with trials where the item was recognized as studied, but the source was incorrectly reported (often called No Source Hits). This contrast may identify cognitive processes involved in the retrieval of contextual information from the study event, although it should be noted that the specific aspect of source being probed may influence these cognitive processes (Danker & Anderson, 2010; Johnson et al., 2009). These recollective processes are central not only to cognitive models of recognition (Yonelinas, 2002) but also to models of free recall (Polyn, Norman, & Kahana, 2009a; Sederberg, Howard, & Kahana, 2008; Howard & Kahana, 2002), in which the contextual information retrieved during a particular recall event helps to guide the subsequent memory search. These models suggest that the cortical regions mediating episodic recollection should be commonly recruited across recognition and recall tasks.

To identify familiarity-related neural processes, researchers have contrasted activity for trials where the item was successfully recognized without recollection (the No Source Hits described above) with trials on which a novel lure was successfully detected (Correct Rejections; e.g., Wheeler & Buckner, 2004). Although this comparison should identify neural signals related to a mnemonic familiarity signal, other processes recruited during recognition may also be reflected in this contrast (Wagner, Shannon, Kahn, & Buckner, 2005). For example, one might retrieve contextual information that does not specify the relevant source information. Furthermore, decision processes involved in determining whether the probe item was from the targeted temporal context (i.e., the study list) may also be identified (Mandler, 1980). In free recall, similar decision processes may be engaged to determine whether a remembered item is from the appropriate temporal context (Lohnas, Polyn, & Kahana, 2015). To the extent that both recognition and free recall tasks rely on a verification process determining whether the retrieved information is from the appropriate temporal context, these networks should show common recruitment across tasks.

By comparing recollective and familiarity contrasts to one another, researchers have revealed a number of functional dissociations across multiple cortical systems, which have been taken as evidence that distinct neural mechanisms contribute to these processes during recognition tasks (Ranganath & Ritchey, 2012; Diana et al., 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Brown & Aggleton, 2001). The hippocampus (Ranganath, Cohen, Dam, & D'Esposito, 2004; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000) as well as cortico-hippocampal networks spanning prefrontal and posterior parietal cortex (Hayama, Vilberg, & Rugg, 2012; Okada, Vilberg, & Rugg, 2012; Vilberg & Rugg, 2008) have been shown to be selectively identified by recollection contrasts. The familiarity contrast, on the other hand, seems to selectively identify cortical structures in anterior medial-temporal lobe (MTL), such as perirhinal cortex (Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011; Daselaar, Fleck, Prince, & Cabeza, 2006; Henson, Cansino, Herron, Robb, & Rugg, 2003). Additional dissociations have been observed across frontal and parietal cortices. In pFC, lateral regions have been associated with familiarity processes, and anterior medial regions with recollective processes (Yonelinas, Otten, Shaw, & Rugg, 2005). In parietal cortex, activity near the lateral intraparietal sulcus increases with the perceived familiarity of a stimulus (Hutchinson et al., 2014; Sestieri et al., 2014; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Wagner et al., 2005; Yonelinas et al., 2005), whereas the left posterior parietal activity in the vicinity of the angular gyrus has been associated with recollection of prior experiential details (Hutchinson et al., 2014; Hayama et al., 2012; Okada et al., 2012; Vilberg & Rugg, 2012).

Given its comprehensive spatial coverage of the brain, fMRI is well suited to characterize whether the processing mechanisms engaged during free recall are shared with, or distinct from, those engaged for recollection and familiarity (Mather, Cacioppo, & Kanwisher, 2013). A similar approach has been taken in recent work, demonstrating shared engagement of neural circuits across both visual search and memory search tasks (Cabeza et al., 2011) as well as recognition and cued recall tasks (Hayama et al., 2012; Okada et al., 2012). Although a number of recent studies have characterized the neural correlates of internally directed search during free recall (Kragel & Polyn, 2015; Kragel et al., 2015; Shapira-Lichter et al., 2012, 2013; Long et al., 2010), there have been no studies directly comparing free recall with recognition.

In much of the prior work comparing neural engagement across different tasks, univariate statistics have been employed to determine whether the same cortical regions reliably increase (or decrease) in activation for each of the tasks. Although these conjunctive analyses provide a starting point for cross-task comparisons of neural engagement, they do not address whether the broader pattern of engagement and disengagement across multiple brain regions is preserved across tasks. Multivariate pattern analysis (MVPA; Norman, Polyn, Detre, & Haxby, 2006) can be used to characterize the topography of neural responses both within and across brain regions. This allows one to ask whether the global pattern of brain response is similar for two independent contrasts, strengthening the form of inference one can make regarding the significance of overlapping activation (Peelen & Downing, 2007). MVPA has been used to compare topographic patterns of neural activity across experimental conditions in a number of cognitive domains, including task performance (Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009) and subjective remembering (Rissman, Greely, & Wagner, 2010). Recent demonstrations of between-subject decoding show that MVPA can be used to determine whether patterns of neural activity (and the cognitive processes presumed to be reflected

therein) are common across individuals (Clithero, Smith, Carter, & Huettel, 2011; Haxby et al., 2011).

In this study, we employed a within-subject fMRI design to determine whether the cognitive processes supporting the retrieval of item and contextual information during a source recognition task also support retrieval during a free recall task. In previous work, we examined the free recall portion of these data, identifying transient activation of the hippocampus and multiple cortical networks when individual items are recalled (Kragel & Polyn, 2015). In the present work, we test the degree to which retrieval in the free recall task and the source recognition task are mediated by similar processes, despite inherent differences between the two. During the recognition task, we identified neural activity associated with (1) the recollection of source information and (2) the recognition of a studied item in the absence of correct source retrieval. Using univariate convergence and multivariate decoding analyses, we compared brain activity in this recognition task to the brain activity recorded during free recall.

METHODS

Participants

Twenty right-handed, native English speakers (12 women) with a mean age of 22.5 years ($SD = 3.8$ years) from the Vanderbilt University community participated in the study. Participants were compensated $20/hr, with the potential to earn up to an additional $10 contingent on task performance. Informed consent was obtained in accordance with the Vanderbilt University Institutional Review Board.

Behavioral Methods

The experiment consisted of 12 fMRI runs across two sessions, with each run containing three phases of interest:

study, retrieval, and control tasks (Figure 1). During the study period, participants studied lists of 24 items. After each study list, participants performed either a free recall test or a source recognition test. Each session included three free recall lists and three source recognition lists; the conditions were pseudorandomly ordered within each session. Stimulus presentation and recording of responses were implemented on a laptop using PyEPL (Geller, Schleifer, Sederberg, Jacobs, & Kahana, 2007).

During the study period, each presented word was studied with one of two semantic orienting tasks. Within each list, participants were required to judge either the animacy or size of a stimulus presented on the screen (see Polyn, Kragel, Morton, McCluey, & Cohen, 2012, which describes multivariate analyses of task-specific activity in these data, for details). Before each study item, a cue appeared on the screen for 700 msec to indicate which orienting task would apply to the upcoming stimulus. Presentation of a fixation cross followed the task cue for a duration of 300 ± 100 msec, followed by presentation of a study item for 2500 msec. A fixation cross was displayed following the presentation of each studied item for a duration ranging between 500 and 5000 msec. The order of encoding tasks was pseudorandomly determined, with the constraint that no task judgment was repeated more than six consecutive times, and each task was used for half of the items studied on each list.

During the source recognition portion of the task, participants were presented with lists of 32 stimuli, containing 16 targets (drawn evenly from both encoding tasks on the prior study list) and 16 novel lures. Probe stimuli were presented for a duration of 2500 msec, and participants indicated whether the probe stimulus was encoded using the size task or animacy task, or was a novel item. Following the presentation of a fixation cross (300 ± 100 msec), a cue was presented to indicate to the

Figure 1. Experimental paradigm. A sample encoding trial is depicted in the left column, showing the task cue for the animacy judgment, followed by a sample stimulus. The middle column depicts the recall cue, which was paired with an auditory tone, that initiated the recall period. A sample source recognition trial is depicted in the right column, in which the participant must first judge whether the probe was encoded under the size task or animacy task, or was a novel lure. Following this period, participants were cued to make a confidence rating of their previous response. ITI, intertrial interval.

participant to make a confidence judgment on a 3-point scale. Presentation of this cue lasted for a duration of 2500 msec, followed by an intertrial interval of 500 to 5000 msec. All responses made during the encoding and source recognition period were made with either the first, second, or third fingers of the right hand on a response pad. Button-to-response mappings were counterbalanced across trials to control for confounding factors in RTs.

During the beginning of the recall period, a recall cue was presented in the form of a row of asterisks displayed for a 500-msec duration, concurrent with the presentation of an audio tone (800 Hz). Following presentation of the recall cue, participants recalled items studied on the most recent list, in any order. Another tone and row of asterisks indicated the end of the 75-sec recall period. Vocal responses were recorded using a scanner-safe microphone (Resonance Technologies, Inc., Northridge, CA) and scored using *PyParse* (Solway, Geller, Sederberg, & Kahana, 2010) and *Penn TotalRecall* (memory.psych. upenn.edu/TotalRecall).

Following the retrieval phase of the task (either recognition or recall phases), participants performed a speech control task. Novel items were presented in the same format as in the encoding period, for a duration of 2 sec, followed by an ISI of 4 sec. Participants read the presented word aloud, and responses were annotated following the procedures used in the recall period. Each participant performed 18 speech control trials across the study.

fMRI Methods

Data Collection and Preprocessing

Images were collected on an Intera Achieva 3T system (Philips Medical System, Best, the Netherlands) at the Vanderbilt University Institute for Imaging Science. An MP-RAGE sequence was used to collect whole-brain structural scans (repetition time = 2500 msec, echo time = 4.38 msec, voxel size = 1.0 × 1.0 × 1.0 mm, flip angle = 8°, field of view = 256 mm). Functional data were collected using an EPI pulse sequence (repetition time = 2000 msec, echo time = 30 msec, voxel size = 3.0 × 3.0 × 3.6 mm, flip angle = 75°, field of view = 192 mm).

Data were processed using SPM8 (Wellcome, Department of Cognitive Neurology, www.fil.ion.ucl.ac.uk). Prior to preprocessing of functional images, the first four volumes of each run were discarded to allow for equilibration of scanner signal. Functional images were realigned to the first scan of each run, correcting for head motion. Mean functional images from each run were coregistered to structural images, allowing normalization to Montreal Neurological Institute (MNI) stereotactic space using the unified segmentation based approach (Ashburner & Friston, 2005). Functional data were resampled to 3-mm cubic voxels and spatially smoothed with an 8-mm FWHM Gaussian kernel.

General Linear Modeling

The general linear model (GLM), as implemented in SPM8, was utilized to determine whether cortical regions associated with the processes of recollection or familiarity were engaged during memory retrieval in the free recall task. A single GLM was constructed, containing individual regressors to model recognition and recall trials.

Trial types of interest during the source recognition task included retrieval of source information (Source Hits), item recognition in the absence of correct source recollection (No Source Hits), and identification of novel lures (Correct Rejections). Trials in which participants failed to detect novel lures (False Alarms) were additionally modeled; however, they were not used in second-level analyses. Modeling of trials during the recognition task focused on construction of contrasts related to the retrieval of mnemonic information. These comparisons, described below, control for multiple differences between the recognition and recall tasks, including the visual memory probe, manual response selection, and confidence ratings. As such, estimation of the neural response to confidence judgments was omitted from analysis. Two trial types of interest were used to identify changes in BOLD response associated with recall-related processing. One regressor was used to estimate transient activity associated with correct recall of list items (Recalls), and an additional regressor was used to estimate changes in the BOLD signal during the speech control task (Speech). Incorrect recalls (intrusions of nonstudied items) were rare and not analyzed. By comparing overt recalls to the speech control task, we constructed an estimate of transient activity related to the recall of individual list items.

Additional regressors were included to model neural activity during the encoding period. The neural response on each event of interest was modeled as a delta function coincident with the onset of each event (either stimulus presentation or the onset of vocalization). The BOLD response for each event was modeled by convolving each series of delta functions with the canonical hemodynamic response function and its temporal derivative. An additional block regressor of 75-sec duration was included to model sustained differences in activation across the recall period (see Kragel & Polyn, 2015, for analysis of recall period dynamics). Six covariates were included in first-level models, corresponding to motion parameters to estimate movement in x, y, and z dimensions, as well as rotation, pitch, and yaw. An autoregressive AR(1) model was implemented to account for temporal autocorrelations in observed BOLD time series. Prior to parameter estimation, BOLD time series were high-pass filtered with a cutoff at 128 sec to remove low-frequency components in the time series.

Following first-level estimation of β coefficients, linear contrasts of interest were computed for each participant, resulting in a single image per trial type per participant. Post hoc classification of events according to memory

Table 1. Response Proportions and RTs (in msec) during the Source Recognition Task

Response	Confidence	Proportion (SEM)			RT (SEM)		
		Size	Animacy	Novel	Size	Animacy	Novel
Size	Low	1.13 (1.64)	6.65 (6.83)	1.56 (2.47)	1569 (230)	1546 (384)	1768 (377)
	Medium	13.26 (8.31)	14.78 (9.21)	1.51 (3.96)	1534 (313)	1616 (316)	1740 (238)
	High	68.97 (15.23)	6.92 (8.81)	0.52 (0.79)	1338 (313)	1482 (325)	1487 (458)
Animacy	Low	3.96 (3.58)	3.74 (5.73)	1.20 (2.30)	1579 (350)	1711 (347)	1625 (426)
	Medium	4.86 (4.60)	13.02 (7.39)	0.21 (0.54)	1630 (372)	1633 (350)	1882 (247)
	High	2.56 (2.29)	46.38 (15.97)	0.42 (0.71)	1596 (370)	1359 (332)	1155 (224)
Novel	Low	2.66 (3.19)	2.71 (3.58)	1.98 (4.30)	1415 (419)	1423 (452)	1334 (403)
	Medium	0.81 (1.54)	1.70 (1.90)	10.21 (14.68)	1681 (381)	1703 (336)	1276 (359)
	High	1.26 (2.08)	3.19 (3.10)	81.15 (22.36)	1148 (443)	1193 (376)	1015 (277)

status led to an imbalanced design, with an increasing number of trials per list for No Source Hits (mean = 3.2, range = 1.2–6.5), Source Hits (mean = 11.7, range = 8.3–13.7), and Correct Rejections (mean = 15.0, range = 9.5–16.0). Inference using random effects analysis is robust to design imbalances of this nature (Friston, Stephan, Lund, Morcom, & Kiebel, 2005). Second-level analyses were conducted using paired t tests for each contrast of interest, corresponding to source recollection (Source Hits vs. No Source Hits), item familiarity (No Source Hits vs. Correct Rejections), and item recall (Recalls vs. Speech).

Effects were considered significant if they survived an uncorrected voxelwise threshold of $p < .001$ and an extent threshold, k, of at least 38 voxels. This cluster extent threshold was determined based on Monte Carlo analysis of statistical maps, using *3dclustsim* in AFNI (afni. nimh.nih.gov/pub/dist/doc/program_help/3dClustSim. html), and resulted in a cluster-level α = 0.05, corrected for multiple comparisons across the whole brain. Statistical maps depicting the overlap between processes of interest were constructed by inclusively masking the item recall t map with either the recollection or familiarity-based maps. Thresholding the individual t maps at this level ensures a test of the conjunction null at $p < .001$ (Nichols, Brett, Andersson, Wager, & Poline, 2005).

Multivariate Pattern Analyses

Two separate applications of MVPA were implemented using patterns of activity across either the whole brain or across a set of functionally defined ROIs defined by the overlapping neural regions identified in the previously described univariate convergence analysis. Regardless of the features used for analysis, each participant's mean response for conditions of interest (i.e., the contrast images resulting from the first-level analysis) were converted into z scores (i.e., standardized across voxels) and used as features for classifier training and evaluation. We then used

LIBSVM software, implemented in MATLAB (www.csie. ntu.edu.tw/~cjlin/libsvm), to construct a linear support vector machine (SVM). Parameterization of the SVMs was determined using a twofold, nested cross-validation approach (Mumford, Turner, Ashby, & Poldrack, 2012; Pereira, Mitchell, & Botvinick, 2009), determining the value of the regularization parameter, C, of each classifier. Following parameterization, a leave-one-out cross-validation approach was used to evaluate classifier performance. Classifiers were trained on patterns of neural activity from all but one participant, and performance was evaluated on the remaining participant's patterns.

Significance of classifier performance was determined using a one-tailed binomial test (Pereira et al., 2009), determining the probability that the observed predictions were generated by chance (assuming the probability of predicting either class was .5). This statistical model assumes that test cases are independent of one another and can lead to false positives under circumstances where this is not the case (Stelzer, Chen, & Turner, 2013). However, folds of our cross-validation procedure are implemented across participants and as such are unlikely to be dependent upon one another. Whole-brain classification results were considered significant at $p < .05$, uncorrected. Models using functionally defined ROIs for feature selection were considered significant after surviving a threshold of $p < .05$, Bonferroni corrected for the number of classifiers tested, considering both the number of input contrasts as well as the feature spaces that were tested. Uncorrected p values are reported in the text.

RESULTS

Behavioral Results

Source Recognition

During the recognition test, participants were sensitive to the mnemonic status of the probe, with a d' of 3.44 ±

0.18 (mean ± *SEM*). Table 1 describes the observed relationship between confidence ratings and recognition performance, showing higher confidence for correct source judgments than incorrect judgments. Hit rates for trials endorsed with low confidence were significantly lower than trials endorsed with medium ($t(17) = -2.84$, $p = .011$) and high ($t(17) = -3.60, p = .002$) confidence. Correct rejection rates also varied depending upon the associated confidence response, with paired *t* tests revealing significant differences in correct rejection rate between low and medium ($t(11) = -5.93, p = .0001$), low and high ($t(13) = -8.05, p < .0001$), and medium and high ($t(15) = -2.25, p = .039$) confidence judgments. These analyses were restricted to the subset of participants who responded at a given level of confidence, as the full range of confidence values were not utilized by all participants (e.g., Correct Rejections were rarely endorsed with low confidence).

Participants performed above chance levels on source judgments of items endorsed as old, with a proportion correct of $0.73 ± 0.02$ ($t(19) = 9.99, p < .0001$). Hit rates on source correct trials were greater than on trials in which participants failed to recover the source of the encoded item ($t(19) = 12.89, p < .0001$), demonstrating that retrieval of source information influenced both recognition and confidence judgments. Furthermore, source judgments were more accurate during high (relative to medium) confidence decisions ($t(19) = 9.51, p < .0001$). Low-confidence decisions were associated with impaired source recognition when compared with medium ($t(17) = -5.68, p < .0001$) and high ($t(17) = -13.44, p < .0001$) confidence responses.

Free Recall

On average, participants recalled $42 ± 0.03\%$ (mean ± *SEM*) of the studied items. Primacy and recency effects were observed as an advantage in recall for the first three ($t(19) = 5.31, p < .0001$) and last three ($t(19) = 5.91$, $p < .0001$) serial positions. Recall errors were rarely observed, with extralist intrusions occurring on average 0.35 (0.22–0.78 95% CI) times per list. Prior list intrusions were only made by four participants, with an average of 0.2 (0.05–0.55 95% CI) errors per recall list. Additional behavioral analysis of the recall data collected in this experiment is described in previous work (Polyn et al., 2012).

fMRI Results

Univariate Analyses

To investigate whether the neural substrates that support item familiarity and source recollection during recognition tasks are recruited during free recall, we employed a series of GLM-based analyses that allowed us to make forward inferences (Henson, 2006) regarding the cognitive processes that support episodic retrieval. First, we

determined which regions were associated with item familiarity in the absence of source recollection (by contrasting No Source Hit trials with Correct Rejection trials). Next, we identified regions where activity was associated with accurate source recollection (by contrasting Source Hit trials with No Source Hit trials). We then implemented a convergence analysis to determine whether any regions related to item familiarity or source recollection were also engaged for retrieval during free recall. We identified regions associated with correct retrievals during memory search (by contrasting recall events in free recall with events from a speech control task) and looked to see whether there was common engagement between this free recall contrast and either the item familiarity or source recollection contrast. We note that, although the speech task allowed us to control for neural activity associated with vocalization, it is not a perfect control task, as it involves items being visually presented to the participant. This was done to minimize the engagement of memory processes during the speech task. In the following section, we examine the neural patterns associated with the speech control task in more detail.

Figure 2A depicts clusters of activation that were sensitive to item familiarity. Increased activity during the detection of previously studied items (in the absence
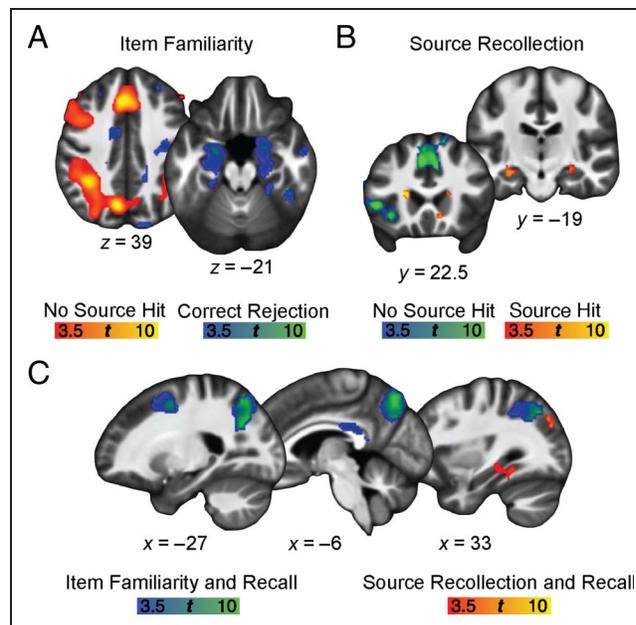

Figure 2. Overlapping neural substrates during source recognition and free recall. Differences in activity between (A) hits in the absence of source recollection and correct rejections and (B) hits with and without source recollection. (C) Convergence analysis of free recall and source recognition effects. The statistical map for Recall > Speech is displayed in regions exhibiting either item recognition or source recollection effects. Statistical maps are rendered on the group-mean T1 anatomical image, with a cluster-wise threshold of $p < .05$ corrected for the whole-brain volume. Slices are labeled with their corresponding MNI coordinates.

Table 2. Item Familiarity Sensitive Regions

Contrast	Gyrus (Hemisphere)	BA	k	Coordinates (x,y,z)	t
No Source Hit > Correct Rejection	Precuneus (L)	7	1472	−6,−70,43	11.81
	Inferior parietal lobule (L)	40		−45,−31,40	5.72
	Claustrum (L)		2662	−30,23,−5	11.62
	Medial frontal gyrus (L)	6		−6,23,43	10.81
	Middle frontal gyrus (L)	9		−48,23,28	10.07
	Superior frontal gyrus (R)	6		24,14,64	4.90
	Superior frontal gyrus (L)	6		−27,2,70	4.18
	Insula (R)		145	36,23,−5	7.99
	Caudate (R)		51	12,5,−2	6.95
	Thalamus (L)		225	−9,−13,1	6.79
	Posterior cingulate (L)	23	88	−6,−34,25	6.34
	Inferior Parietal Lobule (R)	40	194	36,−46,46	5.80
	Middle frontal gyrus (R)	6	48	27,−1,52	5.06
	Middle frontal gyrus (R)	9	102	42,29,28	4.60
Correct Rejection > No Source Hit	Fusiform gyrus (R)	37	7372	45,−43,−17	10.34
	Parahippocampal gyrus (L)	19		−42,−43,−8	8.89
	Cuneus (L)	30		−27,−76,10	7.86
	Parahippocampal gyrus (L)			−21,−4,−23	7.64
	Insula (R)	13		36,−1,13	7.60
	Superior temporal gyrus (L)	22		−54,−10,4	7.34
	Caudate (L)			−18,20,10	7.30
	Parahippocampal gyrus (R)	34		24,−1,−20	6.91
	Middle temporal gyrus (R)	21		60,−7,−23	6.80
	Postcentral gyrus (R)	3	1190	33,−25,46	6.67
	Subgyral (L)	7		−21,−40,58	6.08
	Middle frontal gyrus (R)	8	45	30,35,37	5.10

BA = Brodmann's area; L = left; R = right. k = cluster extent, in voxels. Brodmann's areas and anatomical locations are approximate. t values are reported for peaks within each cluster located at least 8 mm apart for each contrast. Coordinates are given in MNI space.

of a correct source judgment) was observed within widespread cortical regions, including lateral and medial parietal cortex, fronto-opercular cortex, and dorsal anterior cingulate. Detection of novel items (i.e., Correct Rejections) was accompanied by increased activity within bilateral anterior MTL regions, including hippocampus, amygdala, and surrounding rhinal cortex. A full description of the clusters identified by this analysis, as well as peaks in activation, is described in Table 2.

Figure 2B depicts clusters that were sensitive to source recollection during the recognition task. This contrast identified activation within bilateral MTL, spanning hippocampus and parahippocampal cortex (peak reported in Table 3), that was sensitive to the retrieval of source

information. Relative to correct source judgments, incorrect source judgments demonstrated greater levels of activity within dorsal anterior cingulate and multiple left-lateralized prefrontal regions, spanning both dorsal and ventral pFC (Table 3 contains a complete listing of identified clusters).

Finally, Figure 2C presents the results of the convergence analysis used to determine which cortical regions were associated with either source recollection (Source Hits > No Source Hits) or item familiarity (No Source Hits > Correct Rejections) and with retrieval-related processing during the free recall task (Recalls > Speech). A cluster spanning right posterior hippocampus and adjacent parahippocampal cortex was engaged for

both free recall and source recollection. Multiple prefrontal and parietal regions were engaged for both free recall and item familiarity. Table 4 provides full details on the identified clusters. We did not observe overlap between free recall and item familiarity activity within the MTL. No regions demonstrated activity related to all three effects (free recall, item familiarity, and source recollection).

Multivariate Decoding Reveals Cognitive Processes Engaged during Free Recall

The GLM-based analysis described above shows that there are shared neural substrates between free recall and both item familiarity and source recollection processes. Although a convergence analysis can identify sets of voxels responsive to more than one contrast, it does not test whether distributed patterns of neural activity elicited during free recall match the patterns identified with the item familiarity and source recollection contrasts. To address this, we performed a series of multivariate decoding analyses, starting at the level of the whole brain and then within the individual clusters identified in the convergence analysis above.

For each of these analyses, two classifiers were constructed: one trained to differentiate between patterns of neural activity associated with the presence or absence of successful source recollection (i.e., distinguishing Source Hits from No Source Hits) and another trained to differentiate between patterns of neural activity associated with item familiarity and novelty in the absence of source recollection (i.e., distinguishing No Source Hits from Correct Rejections). Then, we presented each trained classifier with the patterns of activity created from our free recall contrast (recall events vs. speech events). As such, the output of the source recollection classifier indicates whether the free recall pattern is more similar to the class of successful, or unsuccessful, source recollection patterns. Similarly, the output of the item familiarity classifier indicates whether the free recall pattern is more like the detection of a previously studied item or a novel lure. As described in Methods, we used an across-subject cross-validation technique to ensure that the classifier was not influenced by idiosyncratic characteristics of individual subject activity patterns.

We first examined each classifier to determine whether it could reliably distinguish the two classes of patterns at the whole-brain level. The item familiarity classifier was reliably able to distinguish successful recognition of a target (without source recollection) from successful rejection of a novel lure (accuracy = 0.93, $p < .0001$, 95% CI [0.88 0.96]). These high levels of performance were obtained for both classes: item recognition without source details (sensitivity = 0.95, $p < .0001$, 95% CI [0.87

Table 3. Source Recollection Sensitive Regions

Contrast	Gyrus (Hemisphere)	BA	k	Coordinates (x,y,z)	t
Source Hit > No Source Hit	Insula (L)	13	220	−30,2,19	6.22
	Parahippocampal gyrus (L)	37	182	−33,−46,−8	6.21
	Lentiform nucleus (R)		257	27,2,1	6.13
	Postcentral gyrus (R)	3		33,−25,46	5.19
	Caudate (L)		65	−18,26,10	5.77
	Subcallosal gyrus (R)	34	583	18,8,−20	5.68
	Fusiform gyrus (R)	20		33,−37,−17	5.39
	Parahippocampal gyrus (L)			−27,−16,−17	5.01
	Superior occipital gyrus (R)	19	145	36,−79,34	5.32
	Middle temporal gyrus (R)	39		48,−55,7	4.55
	Paracentral lobule (L)	7	40	−18,−40,55	4.70
No Source Hit > Source Hit	Cingulate gyrus (R)	32	496	3,29,31	6.49
	Superior frontal gyrus (R)	6		24,17,67	5.18
	Subgyral (L)	6		−24,11,52	4.62
	Middle frontal gyrus (L)	9	53	−36,26,25	5.64
	Precentral gyrus (L)	44	266	−45,20,1	5.41
	Middle frontal gyrus (L)	9		−54,11,37	4.47

BA = Brodmann's area; L = left; R = right. k = cluster extent, in voxels. Brodmann's areas and anatomical locations are approximate. t values are reported for peaks within each cluster located at least 8 mm apart for each contrast. Coordinates are given in MNI space.

Table 4. Regions Demonstrating Overlapping Source Recollection and Item Familiarity Effects during Free Recall

Contrast	Gyrus (Hemisphere)	BA	Extent	Coordinates (x,y,z)	t
Recall and source recollection	Middle occipital gyrus (R)	19	55	33,−79,28	9.49
	Anterior cingulate (R)	25	90	9,20,−11	7.69
	Fusiform gyrus (L)	37	38	−45,−43,−20	6.49
	Parahippocampal gyrus (R)	19	70	42,−49,−8	6.40
Recall and item familiarity	Precuneus (R)	7	1195	18,−67,49	10.00
	Precuneus (L)	7		−24,−70,49	9.12
	Inferior parietal lobule (L)	40		−45,−28,46	8.45
	Precuneus (R)	19	178	30,−70,40	9.04
	Inferior parietal lobule (R)	40		45,−34,46	3.88
	Middle frontal gyrus (L)	6	426	−24,−1,46	8.00
	Middle frontal gyrus (L)	9		−54,23,34	4.59
	Posterior cingulate (R)	23	83	6,−31,22	6.08
	Middle Frontal Gyrus (R)	9	74	45,32,19	5.65
	Middle frontal gyrus (R)	6	41	27,2,49	5.52

BA = Brodmann's area; L = left; R = right. *k* = cluster extent, in voxels. Brodmann's areas and anatomical locations are approximate. *t* values are reported for peaks within each cluster separated by a minimum of 8 mm from the item recall (Recalls vs. Speech) contrast. Coordinates are given in MNI space.

0.99]) and detection of novel lures (sensitivity = 0.90, $p < .0001$, 95% CI [0.81 0.95]). Figure 3A shows the average linear SVM weights across the 20 cross-validation folds, with increased activation of left dorsolateral pFC, precuneus, and lateral parietal cortex reflecting detection of a previously encountered memory probe. Increased activity in visual and anterior MTL regions was associated with probe novelty, consistent with the univariate findings depicted in Figure 2A.

The source recollection classifier was also reliably able to distinguish patterns reflecting the presence or absence of accurate source details at the whole-brain level (accuracy = 0.80, $p < .0001$, 95% CI [0.74 0.85]) on an across-subject cross-validation test. Overall classifier performance was above chance for both correct source judgments (sensitivity = 0.90, $p < .0001$, 95% CI [0.81 0.95]) and incorrect source judgments (sensitivity = 0.70, $p = .021$, 95% CI

[0.60 0.78]). Figure 3B shows the weights from this classifier, identifying regions that contribute to the classification. Consistent with the observed univariate effects, increased activity within the MTL, including right posterior hippocampus and ventromedial pFC, informed the classifier of the recollection of source details. In contrast, increased activity within ventrolateral pFC, dorsal anterior cingulate, and ventral parietal cortex signaled item recognition in the absence of correct source recollection.

We then presented the whole-brain free recall patterns to each of the classifiers. The item familiarity classifier reliably identified the free recall patterns as reflecting correct old (P(No Source Hit) = 0.85, $p = .0002$, 95% CI [0.76 0.91]), rather than novel (P(Correct Rejection) = 0.15, $p = .99$, 95% CI [0.09 0.24]) judgments. In other words, the global topographic pattern of activity associated with free recall of a studied item was quite similar

Figure 3. Patterns of neural activity reflect retrieval processes. SVM weights discriminating (A) item novelty and (B) source recollection during the source recognition task. For visualization, images were transformed to Colin atlas space and rendered onto inflated cortical surfaces (Van Essen, 2002). L, left; R, right.
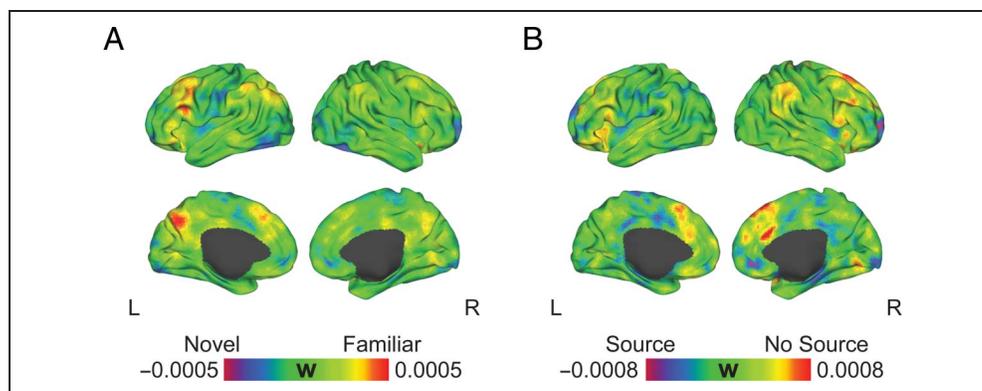
to the pattern of activity associated with successful detection of a studied item in our recognition task. Thus, the neural substrates associated with familiarity-based item recognition are also associated with successful retrieval during memory search.

In contrast, the source recollection classifier did not reliably classify the free recall patterns as similar to either correct source recall (P(Source Hit) = 0.4, p = .75, 95% CI [0.31 0.50]) or incorrect source recall (P(No Source Hit) = 0.6, p = .13, 95% CI [0.50 0.69]). These results suggest that at the level of the whole brain, distinct neural circuits are engaged for successful retrieval during free recall as compared with source recollection, during the recognition task.

This result stands in contrast to our observation of overlapping neural engagement for free recall and source recollection in our univariate conjunction analysis (Figure 2C), suggesting that, despite there being regions of common engagement, there was mismatch between the whole-brain topographic patterns associated with these two processes. One possibility is that there was a good match between free recall and source recollection patterns within the regions identified by the univariate analysis, but that match was overwhelmed by dissimilar patterns in other brain systems. Thus, we carried out a second set of classification analyses, in which the classifiers were trained on just the voxels identified from the univariate conjunction maps from our GLM-based analysis. In other words, the item familiarity classifier was trained on the clusters identified in the item familiarity/free recall conjunction, and the source recollection classifier was trained on the clusters identified in the source recollection/ free recall conjunction. To ensure that feature selection did not bias the output of the classifier, independent conjunction maps were constructed for each fold of the cross-validation analysis.

We trained a source recollection classifier using this scheme—using a subset of features known to exhibit univariate differences in source recollection in a subset of subjects—to discriminate between Source Hits and No Source Hits. Accuracy of this classifier was not significantly different from chance (accuracy = 0.60, p = .077, 95% CI [0.43 0.75]). When this classifier was used to decode the free recall patterns, it reliably identified the patterns as reflecting the absence of correct source information during recall (P(No Source Hit) = 0.85, p < .0001, 95% CI [0.62 0.97]). Although this result should be interpreted cautiously, given the unreliability of the basic source recollection classification, it is consistent with the result of the item familiarity classification analysis: In both cases, free recall patterns were classified as similar to No Source Hit patterns. We carried out an additional classification analysis in which the statistical thresholds from the conjunction analysis were relaxed (to p < $\sqrt{.001}$), increasing the number of features informing the source recollection classifier. The results of this additional analysis were qualitatively identical to those reported

above, providing further support for the idea that activity patterns indicating successful source recollection are not present during free recall.

The item familiarity classifier reliably distinguished No Source Hits from Correct Rejections (accuracy = 0.85, p < .0001, 95% CI [0.70 0.94]). When this classifier was used to decode the free recall patterns, it reliably identified the patterns as reflecting the detection of familiar item information (P(No Source Hit) = 0.85, p < .0001, 95% CI [0.62 0.97]). This is consistent with the results of the whole-brain classification analysis and demonstrates that the functional networks identified in the univariate conjunction analysis have a similar response for item retrieval in free recall and for the detection of a studied item during the recognition paradigm.

A potential issue regarding the interpretation of these findings involves the degree to which the classification results were influenced by the nature of the free recall contrast, which contrasted recall events with events from a speech control task. To minimize memory-related effects in the speech control task, the participants were presented with words that had not been presented before in the experiment and simply read them aloud. However, the possibility remains that these control words elicited some amount of novelty-related processing. To examine this, we created patterns in which both speech trials were contrasted with the implicit baseline of the GLM and conducted a classification analysis in which these patterns were presented to both the source recollection and item familiarity classifiers. These analyses were conducted both at the level of the whole brain and within functionally defined networks of interest.

We observed a slight bias for whole-brain Speech patterns to be classified as novel lures (P(Correct Rejection) = 0.70, p = .02, 95% CI [0.46 0.88]) using the whole-brain classifier; however, this effect did not reach statistical significance when accounting for multiple comparisons (correcting for tests across classifiers and features). It should be noted that the 95% confidence interval overlaps with chance performance. Furthermore, when considering the subset of features within the item familiarity network (Figure 2A), Speech patterns were not reliably classified as novel (P(Correct Rejection) = 0.60, p = .13, 95% CI [0.36 0.81]). When the Speech patterns were presented to the source recollection classifier, there were no reliable effects (all ps > .74) at the whole-brain level or when the features were restricted to the source recollection network. As such, the results of our classification analyses were not driven by novelty effects related to the speech control task.

DISCUSSION

We used fMRI to determine whether free recall and recognition tasks rely on common neurocognitive mechanisms, specifically testing whether item familiarity and source recollection processes commonly associated with

recognition-based tasks are recruited during free recall. Within the MTL, univariate tests revealed overlapping free recall and source recollection engagement in the right posterior hippocampus and parahippocampal cortex. More broadly, there was overlap between free recall and familiarity effects within prefrontal and parietal cortex, including precuneus, the lateral bank of the intraparietal sulcus, dorsolateral pFC, and fronto-opercular regions. The results of this univariate conjunction analysis suggest that both familiarity and recollective processes are engaged during free recall. However, this analysis is sensitive only to overlapping activation between the tasks. To determine whether the broader pattern of neural activity elicited by recollective and familiarity-based processes matched that seen during free recall, we carried out a multivariate pattern classification analysis.

The multivariate analysis demonstrated that whole-brain activity could be used to discriminate correct from incorrect source retrieval and correct recognition (without retrieval of task-specific source details) from correct detection of a novel lure. Inspection of the classifier weights confirmed that the recollection discrimination was influenced by activity within the hippocampus and regions comprising the putative recollection network (Hayama et al., 2012). The familiarity discrimination was influenced by activity in a distributed frontoparietal network, encompassing posterior parietal cortex and multiple prefrontal regions (Figure 3A). These trained classifiers were then presented with images drawn from the free recall period. Although the recollective classifier was agnostic as to whether the free recall patterns were more similar to successful or unsuccessful source recollection, the familiarity classifier reliably classified the free recall patterns as similar to brain patterns in which probe items were correctly identified as studied (in the absence of correct source retrieval). This suggests that the neural substrates supporting familiarity-based retrieval are also recruited during successful retrieval in free recall.

In a number of recent behavioral studies, researchers have examined the potential for familiarity-based processing during memory search in free recall. During the recall period, participants in these experiments indicated for each recall event whether they explicitly remembered studying the reported item (indicating retrieval of contextual information), or whether they simply knew it was from the study list (indicating that the judgment was made in the absence of recollective information; Sadeh, Moran, & Goshen-Gottstein, 2015; Mickes et al., 2013; McCabe et al., 2010). Participants endorse many recalled items as simply "known," suggesting that item familiarity-related processes may be engaged during free recall. Although these studies do not reveal the specific processes commonly engaged across recall and recognition, decades of theoretical work in psychology and cognitive neuroscience present a number of possibilities, as we will review below.

A number of theories of MTL organization propose that anterior MTL cortex is centrally involved in pro-

cessing stimulus familiarity (Ranganath, 2010; Yonelinas, Aly, Wang, & Koen, 2010; Diana et al., 2007; Norman & O'Reilly, 2003). These theories are supported by neuroimaging work showing that this region is more active for novel lures than for studied items during a recognition test (Hayes et al., 2011; Tendolkar et al., 2008; Daselaar et al., 2006; Henson et al., 2003), a finding replicated in the current study. Convergent evidence showing novelty signals in the anterior MTL (specifically the perirhinal cortex) of rodents (Brown & Aggleton, 2001) and non-human primates (Brown & Xiang, 1998) supports these theories. Consistent with these prior studies, we observed a signal in anterior MTL indicating stimulus novelty (i.e., greater for novel lures than studied items) during the source recognition task. However, this region did not show differential activity between successful retrieval in free recall and our speech control task. Rather, regions outside the MTL showed similar activation profiles between the recollection and free recall tasks.

Specifically, we found that frontal and parietal regions showed similar activation patterns between the item familiarity contrast and the free recall contrast, suggesting that similar cognitive processes are engaged in both tasks. These regions have been implicated in a number of cognitive functions that could be engaged during free recall, such as the accumulation of mnemonic information (Wagner et al., 2005), monitoring of retrieved information (Dobbins, Simons, & Schacter, 2004; Rugg, 2004), and biasing of attention to internal representations (Cabeza et al., 2008). A recent study by Hutchinson, Uncapher, and Wagner (2015) suggests that, during uncertain mnemonic decisions, dorsal parietal cortex resolves mnemonic uncertainty via enhanced functional coupling with visual word-form regions involved in representing the mnemonic probe. Given recent evidence that activation of networks anchored in dorsal parietal cortex exhibit increased functional connectivity with posterior midline structures, including the hippocampus and retrosplenial complex during free recall (Kragel & Polyn, 2015; Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2012), it is possible that interactions between these regions reflect attentional processes that influence an internally generated retrieval cue within the MTL.

In addition to revealing activation within dorsal parietal cortex, the free recall and item familiarity contrasts also exhibited overlapping activity patterns across tasks within bilateral regions of the inferior parietal lobe, along the lateral bank of the intraparietal sulcus. Posterior parietal cortex has been hypothesized to be involved in the accumulation of mnemonic evidence required to decide whether a probe was studied (Donaldson, Wheeler, & Petersen, 2010; Wagner et al., 2005). Activity within lateral intraparietal sulcus seems to be sensitive to gradations in item memory strength (Hutchinson et al., 2014, 2015). Additionally, lesions in the vicinity of this region have been shown to impair the sense of vividness, or perceived oldness, of mnemonic information (Hower, Wixted, Berryhill, &

Olson, 2014). Judgment processes allowing one to determine whether a particular item was previously studied appear in a number of theories of memory (Brainerd, Wright, Reyna, & Payne, 2002; Mandler, 1980; Anderson & Bower, 1972), wherein judgments of familiarity are a critical component of both recall- and recognition-based tasks. A recent model of free recall suggests that a similar process is necessary to decide whether a remembered item comes from the appropriate temporal context (Lohnas et al., 2015). These observations raise the intriguing possibility that neural circuitry in lateral parietal cortex subserves evidence accumulation for perceived oldness of active mnemonic representations in a task-general fashion. Neurally constrained computational models of retrieval behavior (e.g., Kragel et al., 2015; Turner, van Maanen, & Forstmann, 2015) provide an ideal framework for future work assessing whether activity in this region is consistent with this computational mechanism.

The evidence regarding functional overlap between source recollection and free recall was mixed. We observed a region within the posterior MTL (spanning right hippocampus and parahippocampal cortex) that was identified in both source recollection and free recall contrasts. This overlapping activity is consistent with the idea that activity within the MTL reflects the reinstatement of contextual information during free recall (Kragel et al., 2015; Manning, Polyn, Baltuch, Litt, & Kahana, 2011) as well as during recognition (Hsieh, Gruber, Jenkins, & Ranganath, 2014; Howard, Viskontas, Shankar, & Fried, 2012). The Complementary Learning Systems model (Norman & O'Reilly, 2003; McClelland, McNaughton, & O'Reilly, 1995) provides a potential computational mechanism for these regions, in the form of pattern completion. Hasselmo and Wyble (1997) describe a computational model of the hippocampal system that utilizes a similar mechanism and accounts for both recognition and recall performance in humans, as well as the effects of neuropharmacological disruption of the system. According to this model, the hippocampus allows for both the retrieval of contextual details during recognition and the retrieval of items given contextual input received via afferent projections from the parahippocampal gyrus during recall. In the Remember/Know free recall paradigm reported by Mickes et al. (2013), "remember" responses could indicate hippocampally mediated retrieval of contextual information, and "know" responses could indicate that only item-specific information was retrieved (supporting the knowledge that the item was studied, but not providing any extra contextual details regarding the prior occurrence). This is consistent with the neurocognitive model of free recall recently proposed by Kragel et al. (2015) in which posterior MTL activity (spanning hippocampus and parahippocampal cortex) indicates the fidelity of the contextual information reactivated when a particular item is recalled. By this account, it is not necessary to posit that separate memory systems are involved in the retrieval of memories labeled "remember" and "know"

by the participant. Rather, there is simply variability in the fidelity or amount of associated contextual information reactivated along with the item representation, and it is this contextual information (or absence thereof) that determines the Remember/Know response (Sadeh et al., 2015).

Our finding that distributed patterns of neural activity associated with source recollection did not match those associated with recall may appear somewhat counterintuitive, given overwhelming evidence that the recollection of episodic information (i.e., contextual retrieval) guides free recall behavior from both computational (Polyn et al., 2009a; Sederberg et al., 2008; Howard & Kahana, 2002) and neuroimaging (Kragel et al., 2015; Howard et al., 2012; Shapira-Lichter et al., 2012; Manning et al., 2011) perspectives. It may be that differences in the demands associated with each task are responsible for the mismatch between source recollection and recall patterns. During source recognition, the participant must retrieve episodic details specifying the encoding task used to process the studied word, whereas during free recall, the participant directly reports the words themselves. Prior examination of the recall portion of this data set suggests that a neural representation of encoding task is retrieved during free recall (Polyn et al., 2012). Associations between task states and encoded items have been shown to influence the organization of retrieved materials during free recall (Polyn et al., 2009a; Polyn, Norman, & Kahana, 2009b), providing further evidence that reinstatement of task-specific contextual information occurs during recall. However, it may be that in free recall, task information is much less important for performance than the successful utilization and retrieval of temporal context information, which ensures that the responses all come from the target list (Lohnas et al., 2015; Howard & Kahana, 2002). During recognition, the determination that an item is familiar is more likely to involve retrieval and assessment of temporal context; in the absence of discriminative source information specifying the encoding task, retrieved temporal information will indicate whether the probe item came from the temporal context of the most recent list.

Conclusion

Using a within-subject design, we demonstrated that neural substrates of source recollection and item familiarity are engaged during performance of the free recall task. Successful retrieval of an item during free recall engaged posterior MTL regions that were also implicated in source recollection processes, as well as posterior parietal and lateral prefrontal regions that were also implicated in item familiarity processes. In contrast to these univariate findings, multivariate decoding analyses suggest that familiarity-related processes, but not source recollective processes, were engaged during free recall. These results

may be challenging for neurocognitive theories proposing that recollective processes that contribute to recognition are similar to those engaged during free recall (Yonelinas, 2002; Mandler, 1980). Instead, the present results show that similar neural substrates support free recall and judgments of recognition in the absence of criterial source retrieval. Finally, the observation that prefrontal and posterior parietal regions showed shared engagement for free recall and for the determination of item familiarity may help us understand the cognitive role of these structures across memory tasks.

Acknowledgments

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