Brain Mechanisms of Successful Recognition through Retrieval of Semantic Context

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Abstract

■ Episodic memory is associated with the encoding and retrieval of context information and with a subjective sense of reexperiencing past events. The neural correlates of episodic retrieval have been extensively studied using fMRI, leading to the identification of a "general recollection network" including medial temporal, parietal, and prefrontal regions. However, in these studies, it is difficult to disentangle the effects of context retrieval from recollection. In this study, we used fMRI to determine the extent to which the recruitment of regions in the recollection network is contingent on context reinstatement. Participants were scanned during a cued recognition test for target words from encoded sentences. Studied target words were preceded by either a cue word studied in the same sentence (thus congruent with encoding context) or a cue word studied in a different sentence (thus incongruent with encoding context). Converging fMRI results from independently defined ROIs and whole-brain analysis showed regional specificity in the recollection network. Activity in hippocampus and parahippocampal cortex was specifically increased during successful retrieval following congruent context cues, whereas parietal and prefrontal components of the general recollection network were associated with confident retrieval irrespective of contextual congruency. Our findings implicate medial temporal regions in the retrieval of semantic context, contributing to, but dissociable from, recollective experience. ■

INTRODUCTION

Episodic memory, the ability to re-experience a past event, can be distinguished from other forms of memory on the basis of two characteristics. One is the processing of context information, such as temporal, spatial, perceptual, or other situational details of an event (Tulving, 1983, 1985). The other is "recollective experience" (Tulving, 2002), which is associated with a subjective sense that an event occurred in one's personal past. Certainly, these two factors are closely entwined, as the subjective experience of recollection depends upon retrieving some aspect of the context in which a past event was encoded. The reinstatement of encoding context in support of this subjective experience may be why recollection-based memory decisions are typically reported with very high levels of confidence (Yonelinas, 2001).

Typically, context is operationalized in terms of multiple characteristics (see Ranganath, 2010a; Nadel, 2008; Mayes, Meudell, & Pickering, 1985), for instance, context includes information that is processed in the background, relative to material that is the target of current processing. Context information is also temporally extended, relative to item information. For example, when reading text, a word is typically encoded in the context of a sentence, such that the meaning of the word is integrated with a discourse representation that has been built up over time (Kintsch, 1988). Many theories propose that recollective experience is a process by which contextual information is integrated, attributed to a source, and framed in a first-person perspective (Ranganath, 2010b; Schacter, Norman, & Koutstaal, 1998; Moscovitch, 1995; Johnson, Hashtroudi, & Lindsay, 1993; Tulving, 1985).

One demonstration of the interplay between context processing and retrieval processing in episodic memory is the encoding specificity principle (Tulving & Thomson, 1973), which states that reinstating the context of a past episode can facilitate retrieval of items studied in that context and, conversely, that an inappropriate context cue can impede retrieval even if the cue is semantically related to the target item. For example, when two words are studied together at encoding, re-presenting one of the words at retrieval helps to reinstate the encoding context and cues recognition of the other word even more effectively than presentation of a strong semantic associate (Tulving & Thomson, 1971). Semantic associations among stimuli have also been used to manipulate contextual congruency between encoding and retrieval. When noun homonyms are modified with adjectives within sentences to bias semantic interpretation (e.g., "strawberry jam"), later recognition is impaired for nouns encountered in the context of a different adjective at retrieval (e.g., "traffic jam"), relative to reinstatement of the same encoding context (Light & Carter-Sobell, 1970). These findings suggest that the

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construction of semantic context during discourse processing can play a potent role in shaping episodic memories.

It is clear that successful episodic retrieval is associated with both the activation of context information and in the integration of context information in a manner that gives rise to recollective experience, but less is understood about the degree to which these two factors may be supported independently in the brain. Medial temporal lobe (MTL) regions, in particular the hippocampus (HC), have long been the focus of research on the neural substrates of episodic memory (Squire, 1992; Scoville & Milner, 1957). Neuropsychological studies additionally identified the importance of PFC for episodic memory (Shimamura, 1995; Wheeler, Stuss, & Tulving, 1995), and more recently, neuroimaging studies have revealed activity in parietal cortex—both laterally, in a ventral posterior region in the vicinity of the angular gyrus (AnG), and medially, in retrosplenial or posterior cingulate cortex (PCC)—during episodic memory retrieval (Shimamura, 2011; Cabeza, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Collectively, the involvement of MTL, medial PFC (mPFC), AnG, and PCC regions has come to be recognized as a "general recollection network," such that activation in this network is reliably increased during retrieval of contextual information (Rugg & Vilberg, 2013; Hayama, Vilberg, & Rugg, 2012; Johnson & Rugg, 2007). However, the different roles assigned to different brain areas within the network are unclear.

There is reason to believe that some components of the general recollection network may be critical for context processing, whereas others may contribute to recollective experience. Although not yet established in fMRI studies, hints at functional dissociations have been observed in the selective deficits of neuropsychological patients. For instance, patients with relatively selective HC damage exhibit deficits in recollection-based recognition (Vann et al., 2009; Quamme, Yonelinas, Widaman, Kroll, & Sauvé, 2004) and deficits in memory for contextual information associated with items (Mayes, MacDonald, Donlan, Pears, & Meudell, 1992). In contrast, patients with lateral parietal lesions often report impairments in the subjective experience of recollection, yet can perform normally on tests of source memory and associative memory that require contextual information (Berryhill, Drowos, & Olson, 2009; Davidson et al., 2008; Simons et al., 2008).

The "Binding of Items and Context" (BIC) model of MTL function (Ranganath, 2010a; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007) provides a framework for understanding the role of HC and other brain regions that might support contextual influences on episodic memory. According to BIC and related models (Montaldi & Mayes, 2010; Davachi, 2006; Eacott & Gaffan, 2005), different MTL subregions represent different aspects of an event—that is, the perirhinal cortex represents item information whereas the parahippocampal cortex (PHC) represents context information. The HC, in turn, is involved in binding items and

context together (Ranganath, 2010a; Eichenbaum et al., 2007). A critical part of the BIC framework is that it only assumes a role for HC and PHC in the retrieval of contextual details, whereas cortical targets of these areas, such as regions in parietal cortex and PFC, are thought to support the constructive processes associated with the subjective experience of recollection (Ranganath, 2010a).

In meta-analyses of fMRI studies, activity in HC and PHC (Spaniol et al., 2009; Diana et al., 2007) and also AnG (Spaniol et al., 2009; Vilberg & Rugg, 2008) has been associated with the factor of retrieval processing representing subjective recollection. However, in these studies, subjective recollection could not be separated from the factor of context processing. Sensitivity to context reinstatement can be assessed independently from recollective experience by manipulating the congruency of cues preceding target items on a recognition test. Previous fMRI studies examining cue–target congruency at encoding (Park & Rugg, 2007) and retrieval (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010) have noted the involvement of dorsal posterior parietal regions associated with attentional effects. These studies did not address, however, whether the factors of retrieval processing and context processing are separable within the general recollection network.

In this study, we used event-related fMRI to identify the brain regions involved in retrieval of semantic context and to disentangle context-related effects from activity more generally related to retrieval success. Before scanning, participants encoded 270 sentences, each of which contained a pair of semantically related words. We predicted that during discourse processing, participants would construct a semantic context linking the words in each sentence. The effects of context reinstatement were then examined during a scanned retrieval phase, in which participants made recognition confidence decisions on each trial for a target word preceded by a studied cue word. On "Congruent Cue" trials, the target was preceded by a semantically related cue that had been studied in the same sentence, whereas on "Incongruent Cue" trials, the target was preceded by a semantically related cue that had been studied in a different sentence. Because the semantic associative strength between cue and target items was matched across trial types, the effects of cueing at retrieval depended upon integration of semantic context at encoding, rather than preexisting semantic associations to the target word.

On the basis of the encoding specificity principle, we predicted that recognition of studied target words should be facilitated on trials when the cue word was studied in the same sentence, thus reinstating the same encoding context at retrieval. In addition to characterizing behavioral effects, we sought to uncover regional specificity within the general recollection network. We predicted that HC and PHC would support contextual influences on episodic retrieval and, as such, should be disproportionately engaged during successful retrieval on trials when encoding context was reinstated. On the basis of evidence from

neuropsychological and TMS studies indicating that parietal areas may support the subjective experience of successful retrieval, rather than the recovery of context information (Yazar, Bergström, & Simons, submitted; Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Davidson et al., 2008), we predicted that activity in parietal areas, and particularly the left AnG, should be associated with confident retrieval irrespective of contextual congruency.

METHODS

Participants

Twenty-two healthy, right-handed adults (19–32 years old; 11 women) were recruited from the University of California at Davis (UCD) community. The research protocol was approved by the UCD Institutional Review Board, and all participants provided written informed consent and were paid for their participation. Data from three participants were excluded from analysis because of chance memory performance or excessive head movement. Results are therefore reported for the remaining 19 participants.

Materials

Stimuli consisted of 180 sets of five words arranged as overlapping semantically related word pairs (e.g., CARD–ACE, CARD–DECK, DECK–WOOD, WOOD–CHOP), with words matched for length (M = 5.6 letters) and Kucera–Francis frequency (M = 46.9) and pairs matched for forward associative strength (M = 0.06) derived from the University of South Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998). To minimize the potentially confounding effect of implicit associative responses on memory (Underwood, 1965), care was taken to exclude highly associated word pairs (forward associative strength > 0.25).

From these stimuli, two sets of 270 sentences were constructed as encoding materials, with each sentence containing one pair of semantically related words (i.e., "critical words," which were always separated by two words that were not functionally related). For example, the sentences "I knew the high CARD was the ACE in my hand" and "The WOOD on the DECK had warped over the years" were produced from the stimulus set referenced above (critical words capitalized here for illustrative purposes only). The sets were matched for sentence length (M = 11.9 words). Each stimulus set also produced three possible cue–target pairs as retrieval materials. Within each pair, the cue item was always one of the two critical words; the target item was then either (1) the other critical word that appeared in the same sentence at encoding (e.g., cue = ACE, target = CARD), (2) another semantically related word that had appeared in a different sentence at encoding (e.g., cue = DECK, target = CARD), or (3) another semantically related but unpresented word (e.g., cue = WOOD, target = CHOP). Two counterbalanced orders ensured that no critical words were presented

more than once at encoding and no target item was presented more than once at retrieval. For example, although both of the sentences referenced above may have been presented to the same participant at encoding, at retrieval participants in one condition would encounter ACE–CARD (cue and target items studied in the same or *congruent* sentence context) whereas participants in the other condition would encounter DECK–CARD (cue and target items studied in different or *incongruent* sentence contexts). Care was also taken to minimize semantic overlap across sentences for noncue and nontarget words.

Design and Procedure

The experiment began with an incidental encoding phase, outside of the scanner, during which 270 sentences were presented sequentially on a computer screen. Each sentence appeared for 4 sec, and participants were instructed to rate its pleasantness on a 6-point scale (from "dislike a lot" to "like a lot") with a button-press response. Participants first completed a brief practice session to become familiar with the response format, but they were not told that their memory would later be tested. Subsequently, the retrieval phase was performed in the scanner, with 270 trials divided into six functional runs. As shown in Figure 1, each trial began with a cue word in lower-case
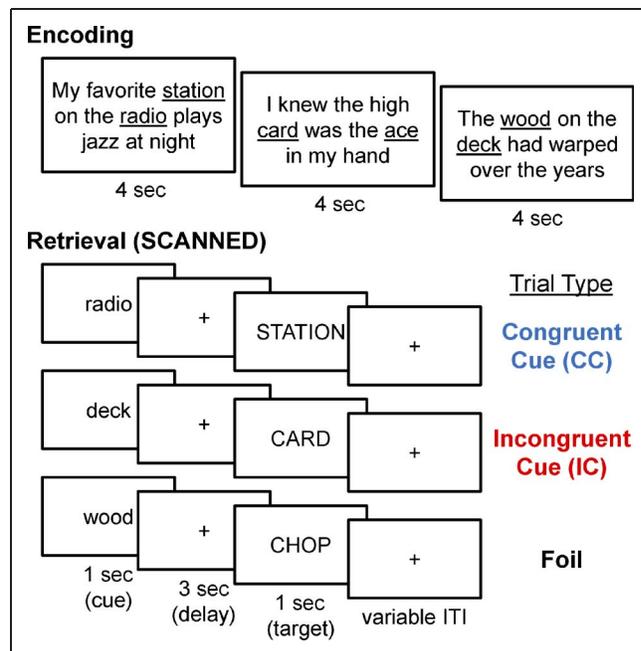
Figure 1. Experimental design. Before scanning, participants encoded a series of sentences, each of which contained a pair of semantically related words (underlined for illustrative purposes only). During scanning, they made recognition confidence decisions for three trial types, all consisting of a target word preceded by a studied cue word. The cue and target words were studied in the same sentence context on Congruent Cue (CC) trials and in different sentence contexts on Incongruent Cue (IC) trials. On Foil trials, the cue word was followed by an unstudied target word.

letters (1 sec), followed by a fixation cross (3 sec) and then a target word in upper-case letters (1 sec). Participants were instructed to make a recognition confidence judgment for the target word on a 6-point scale (from "sure old" to "sure new") with a button-press response. Each run contained 15 trials from each of three trial types: (1) Congruent Cue (CC), in which the cue and target words were studied in same sentence context; (2) Incongruent Cue (IC), in which the cue and target words were studied in different sentence contexts; or (3) Foil, in which a studied cue word was followed by an unstudied target word (see Figure 1). Participants were told that the appearance of each lower-case (cue) word signaled the start of a trial, but they were not told about the congruency manipulation, and task instructions emphasized responding to only the upper-case (target) word on each trial. Trial order was unique across runs and optimized using optseq2 (Dale, 1999), with the intertrial interval varying between 3 and 13 sec (M = 5 sec).

MRI Acquisition and Processing

MRI data were acquired on a 3T Siemens Skyra scanner at the UCD MRI Facility for Integrative Neurosciences. A gradient-echo EPI sequence (repetition time [TR] = 2000 msec; echo time [TE] = 25 msec; flip angle = 90°; field of view [FOV] = 205 mm; 64 × 64 matrix; 34 slices, interleaved; 3.2 mm isotropic voxels) was used to obtain functional images sensitive to BOLD contrast. A total of 232 volumes were collected in each functional run, with the first four volumes discarded to allow for signal equilibration. A gradient-echo field map sequence (TR = 614 msec; TE_1 = 4.92 msec; TE_2 = 7.38 msec; flip angle = 60°; FOV = 256 mm; 80 × 80 matrix) was acquired before the functional runs. An MP-RAGE sequence (TR = 1800 msec; TE = 2.96 msec; flip angle = 7°; FOV = 256 mm; 256 × 256 matrix) was used to obtain high-resolution T1-weighted anatomical images at the end of the scanning session.

Data were preprocessed using SPM8 (www.fil.ion.ucl.ac.uk/spm). Functional images were slice-time corrected using sinc interpolation, realigned and unwarped using the field map parameters, normalized to MNI (Montreal Neurological Institute) space using affine and nonlinear transformations, resliced into 3-mm isotropic voxels, and spatially smoothed using a 6-mm isotropic FWHM Gaussian kernel. For three participants who had errors in field map acquisition, realignment was instead performed using a standard six-parameter, rigid-body transformation.

Analysis

Event-related BOLD responses were analyzed using the general linear model implemented in SPM8, with separate regressors modeling cue and target period activation as a function of trial type (CC/IC) and retrieval success (SureOldHits/OtherHits/Misses). Covariates of interest were constructed by convolving vectors of predicted neural activity with a canonical hemodynamic response function. To account for residual variance because of head movement, realignment parameters were included in the model as covariates of no interest. First-level analysis was performed using the general linear model with a temporal high-pass filter applied to remove frequencies below 0.005 Hz.

To examine task effects within components of the general recollection network, independent functional ROIs were defined using a meta-analysis map generated with the search term "recollection" in the on-line NeuroSynth database (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). Predominant clusters located in PCC (center of mass $[x, y, z] = -1, -52, 28$), mPFC ($-6, 45, 19$), bilateral AnG (LAnG: $-44, -64, 36$; RAnG: $44, -72, 32$), and bilateral MTL were selected for ROI analysis (see Figure 2), on the basis of the recollection network regions described by Rugg and Vilberg (2013). Because the MTL clusters were large enough to encompass several anatomical subregions, they were divided into smaller functional–anatomical ROIs.
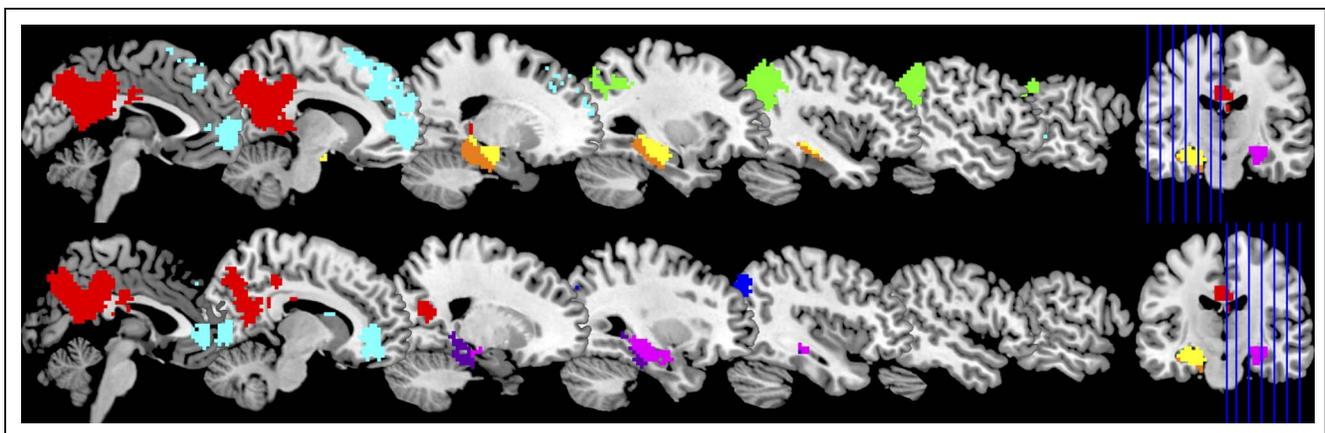
Figure 2. Independently defined general recollection network ROIs. Functional ROIs defined using a reverse inference meta-analysis map for the search term "recollection" in the NeuroSynth database (Yarkoni et al., 2011) include PCC (red), mPFC (cyan), left AnG (green), right AnG (blue), left HC (yellow), left PHC (orange), right HC (magenta), and right PHC (purple). See text for center of mass coordinates.

Table 1. Studied Target Word Response Performance as a Function of Cue Type

	Hits			Misses		
	Sure Old	Old	Guess Old	Guess New	New	Sure New
Mean Proportion of Total Responses						
Congruent cue	0.34	0.22	0.14	0.14	0.11	0.05
Incongruent cue	0.26	0.19	0.15	0.16	0.16	0.06
Mean RT (msec)						
Congruent cue	1390	1879	2186	2351	2047	1873
Incongruent cue	1522	1943	2172	2265	2018	1765

Bilateral HC clusters (L HC: −26, −21, −14; R HC: 29, −20, −13) and bilateral PHC clusters (L PHC: −26, −30, −17; R PHC: 25, −31, −14) were identified within the MTL functional ROIs by computing their intersection with HC and PHC anatomical ROIs from the LONI Probabilistic Brain Atlas (Shattuck et al., 2008). Mean parameter estimates were extracted from the mask images of each recollection network ROI, for each participant, and entered into Contextual Congruency (CC, IC) × Retrieval Success (SureOldHits, Misses) factorial ANOVAs. For exploratory whole-brain analyses, to confirm the reliability of ROI results, contrast images created for each participant were entered into second-level one-sample t tests. Significant regions of activation were identified using an uncorrected threshold of $p < .001$, with a minimum cluster size of five contiguous voxels.

RESULTS

Behavioral Data

On the basis of the encoding specificity principle, we expected that recognition accuracy would be higher and RTs would be faster when cue and target words were studied in the same sentence, thus reinstating the same encoding context at retrieval. Analysis of responses to the studied target words showed that contextual congruency was indeed effective in promoting successful memory retrieval. Overall recognition accuracy (all "old" responses, collapsed across confidence level) was higher for CC ($M = 0.70$) than IC ($M = 0.61$) trials [$t(18) = 5.59, p < .001$], indicating that the reinstatement of semantic context with congruent cues facilitated recognition of studied targets. As shown in Table 1, the effect was driven by high-confidence responses: the average proportion of hits receiving "sure old" judgments was greater for CC than IC trials [$t(18) = 2.67, p < .02$]. Incorporating the rate of false alarms to foils ($M = 0.39$), d' statistics were also higher for CC ($M = 0.84$) than IC ($M = 0.59$) trials [$t(18) = 5.34, p < .001$]. RTs were faster for hits on CC ($M = 1,674$ msec) than IC ($M = 1,818$ msec) trials [$t(18) = 3.84, p < .005$], likewise consistent with a benefit from cue–target congruency.

Estimates of recollection and familiarity were derived from receiver operating characteristic (ROC) curves plotting the proportion of hits versus false alarms for each point on the recognition confidence scale (Yonelinas, 1994), shown in Figure 3. Higher parameter estimates from CC than

Figure 3. Recognition discriminability is higher following context reinstatement. (A) Aggregate recognition ROC plots are shown separately for Congruent Cue trials (blue, solid lines) and Incongruent Cue trials (red, dashed lines). Plots depict averaged hit and false alarm rates across different response criteria. (B) Average estimates of recollection and familiarity derived from ROC curves.
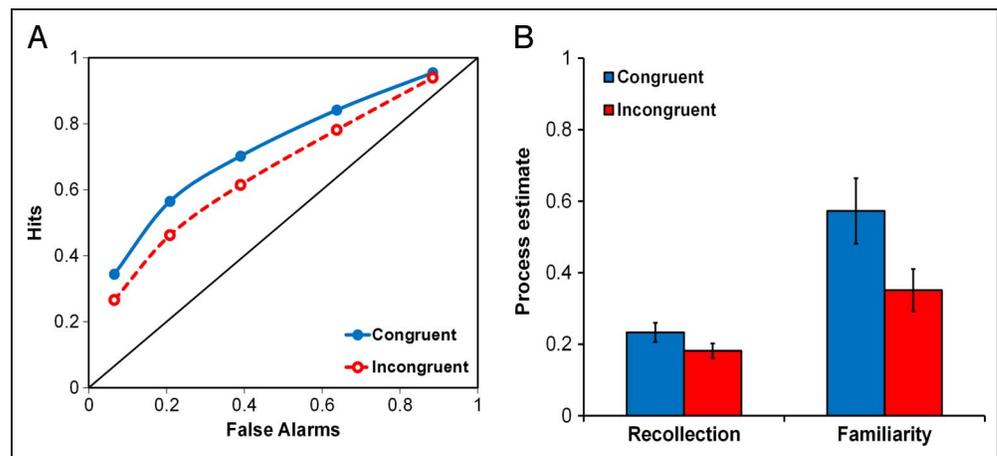
Table 2. Significance Tests from Independently Defined ROI Analyses

	Main Effect of Retrieval Success		Main Effect of Congruency		Retrieval Success × Congruency Interaction	
	$F(1, 18)$	η_p^2	$F(1, 18)$	η_p^2	$F(1, 18)$	η_p^2
L HC	11.08***	.38	1.05	.06	11.96***	.40
R HC	10.30***	.36	2.37	.12	7.37**	.29
L PHC	3.92*	.18	1.68	.09	3.20*	.15
R PHC	0.17	.01	1.20	.06	2.04	.10
L AnG	50.95****	.74	2.29	.11	0.26	.01
R AnG	0.61	.03	1.40	.07	0.10	.01
mPFC	14.00***	.44	1.41	.07	0.15	.01
PCC	3.24*	.15	2.13	.11	.001	<.001

*$p < .10$.

**$p < .05$.

***$p < .01$.

****$p < .001$.

IC trials were found for both recollection [$t(18) = 2.40, p < .03$] and familiarity [$t(18) = 3.79, p < .01$], corroborating the accuracy and RT results reported above. In ROC analysis, chance performance would fall along the diagonal, but target recognition was significantly higher than chance in both conditions ($ps < .001$ in one-sample t tests), as can be seen in the shape of the CC and IC curves.

fMRI Data

We analyzed data from ROIs corresponding to components of the general recollection network (Rugg & Vilberg, 2013), defined based on a meta-analysis map for the search term "recollection" in the NeuroSynth database (see Methods section). For each ROI, mean parameter estimates were entered into Contextual Congruency (CC, IC) × Retrieval Success (SureOldHits, Misses) factorial ANOVAs (see Table 2). First, as shown in Figure 4, the main effect of Retrieval Success (SureOldHits > Misses) on target period activity was significant in L HC, R HC, L PHC, L AnG, and mPFC ROIs (all $ps < .05$) and marginally significant in PCC ($p = .09$), consistent with numerous findings from previous fMRI studies of episodic memory (Rugg & Vilberg, 2013; Spaniol et al., 2009). Second, regional specificity was found in sensitivity to context reinstatement. In bilateral AnG, mPFC, and PCC, there was no reliable interaction between Retrieval Success and Contextual Congruency (Figure 4, bottom row).[1] In contrast, the main effect of Retrieval Success was qualified by an interaction with Contextual Congruency in L HC and R HC ($ps < .05$). In these ROIs, the simple effect of retrieval success was significant on CC trials ($ps < .001$) but not IC trials (Figure 4, top row). In L PHC, the Retrieval Success × Congruency interaction was marginally significant ($p = .06$), and simple effects showed the same pattern.
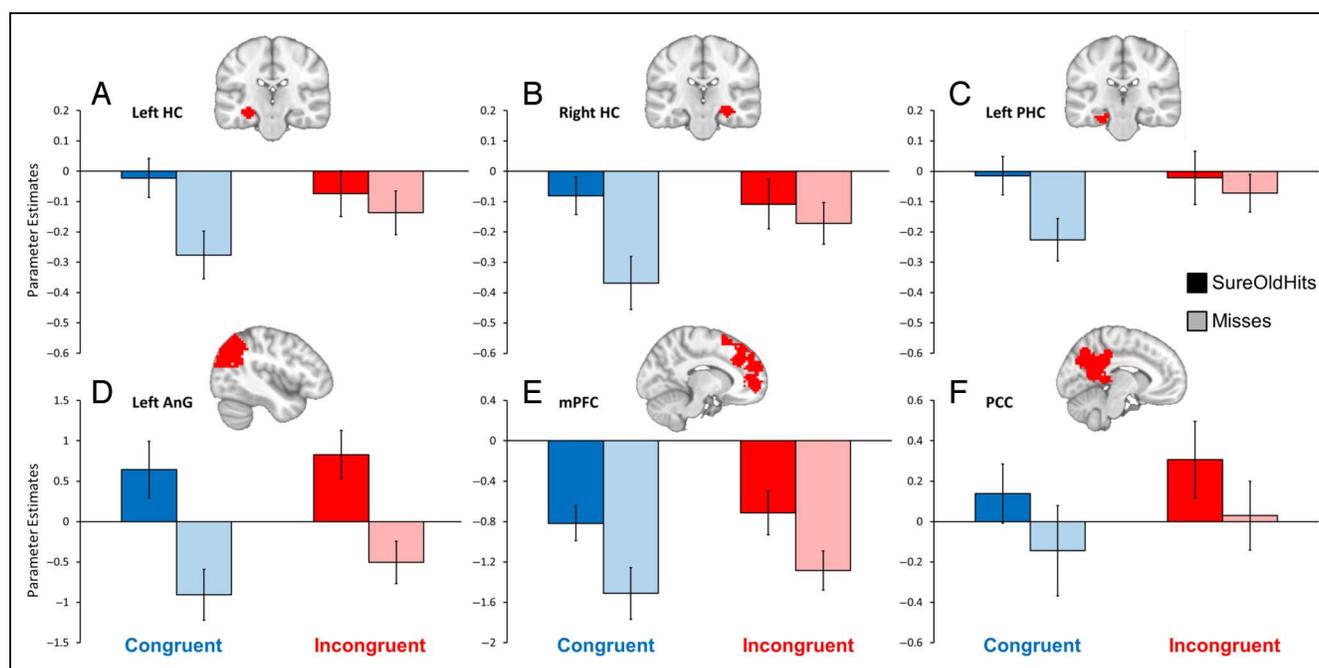
Figure 4. Parameter estimates extracted from general recollection network ROIs. (A–F) Main effects of retrieval success are found throughout the general recollection network, where activity is greater for confident hits (solid bars) than for misses (shaded bars). Sensitivity to context reinstatement is found only in MTL components of the network (A–C), where retrieval success effects are greater on Congruent Cue trials (blue) than Incongruent Cue trials (red). See Table 2 for significance tests.

Figure 5. Exploratory whole-brain analysis. (A) Retrieval success contrast shows significant regions of activation corresponding to the general recollection network. (B) Interaction of retrieval success and contextual congruency shows greater retrieval success effects for Congruent Cue (CC) trials than Incongruent Cue (IC) trials in bilateral PHC and L HC.
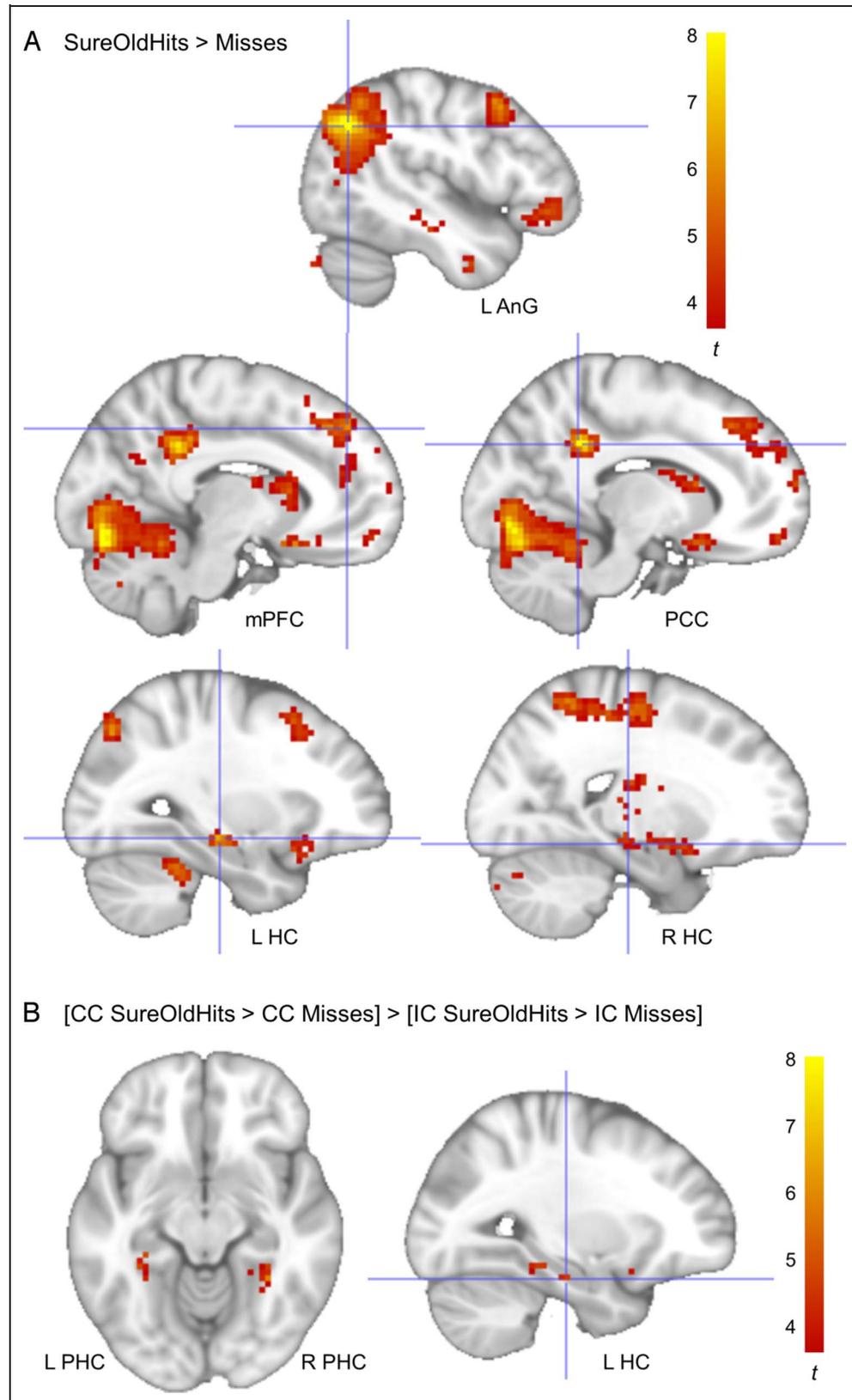
We next conducted exploratory whole-brain analyses to confirm the reliability of the ROI results. A retrieval success contrast of target period activity (SureOldHits > Misses) revealed activation in the general recollection network, including peaks in left AnG, mPFC, PCC, and bilateral HC (see Figure 5A). The interaction between Retrieval Success and Contextual Congruency on target period activity ([CC SureOldHits > CC Misses] > [IC SureOldHits > IC Misses])

Table 3. All Significant Regions of Activation from Retrieval Success × Contextual Congruency Interaction in Exploratory Whole-brain Analysis

	Cluster Size (Voxels)	MNI Coordinates			
		x	y	z	t
Regions within General Recollection Network (see Figure 5B)					
R PHC	23	33	−46	−11	5.85
L PHC	24	−30	−34	−11	4.87
L HC	7	−27	−19	−20	4.58
Regions Not in General Recollection Network					
L OFC	7	−21	17	−17	5.94
R insula	18	36	2	13	5.07
R frontal operculum	15	54	5	10	5.02
R insula	5	39	−13	7	4.66

also identified MTL peaks: in bilateral PHC and L HC, the retrieval success effect was larger for CC targets than IC targets (see Figure 5B), consistent with the ROI analyses implicating these regions in the retrieval of semantic context. Results from the interaction contrast are summarized in Table 3. MTL regions were the only components of the general recollection network to show activation in the whole-brain Retrieval Success × Congruency Interaction; outside of the general recollection network, the interaction contrast identified additional peaks in left OFC (ventral inferior frontal gyrus), right frontal operculum (precentral gyrus), and right insula.

DISCUSSION

In this study, we investigated brain areas associated with the facilitation of episodic memory retrieval through contextual congruency. Behavioral results showed the predicted effects of encoding specificity, with higher recognition accuracy and faster RTs on trials when the semantic context from encoding was reinstated at retrieval. Within the general recollection network (Rugg & Vilberg, 2013), the MTL components (HC and PHC) were disproportionately associated with successful episodic retrieval when context was reinstated, whereas retrieval success effects were independent of context in the parietal and prefrontal components (AnG, PCC, and mPFC).

Numerous fMRI studies of episodic memory have contrasted activity associated with "remember" judgments or high-confidence ratings against activity associated with "know" judgments or low-confidence ratings. These contrasts consistently reveal activation in AnG, HC, and PHC (Spaniol et al., 2009; Vilberg & Rugg, 2008; Diana et al.,

2007). Despite this consistency, there has been ongoing debate about the extent to which such effects reflect processes pertinent to the subjective experience of remembering (Yazar, Bergström, & Simons, 2012; Yonelinas, Aly, Wang, & Koen, 2010; Aggleton & Brown, 1999), the access to contextual information about an encoding episode (Kafkas & Montaldi, 2012; Montaldi & Mayes, 2010; Ranganath, 2010a; Davachi, 2006), or merely the retrieval of information about a strongly encoded item (Smith, Wixted, & Squire, 2011; Wais, 2011). The present results suggest that the answer varies for different regions within the recollection network.

Our findings indicate that, for HC (and to a lesser extent, left PHC), context reinstatement is a critical determinant of recruitment during memory retrieval. Target period activity in HC was significantly higher for confident hits than misses on congruent cue trials, as compared with confidently recognized items that were preceded by an incongruent cue. This result might seem surprising in light of many reports that link hippocampal activity with recollective experience. However, there is a growing body of evidence to suggest that HC contributes to relational memory even when recollection fails. Hannula and Ranganath (2009) used fMRI with concurrent eye tracking and found that HC activity during presentation of a contextual cue predicted subsequent viewing of the item associated with that context, even when explicit recognition decisions were incorrect. Similarly, Yu, Johnson, and Rugg (2012) contrasted recollection-based "remember" responses and familiarity-based "know" responses during a source memory test and found that HC activity reflected the amount of context information retrieved, rather than recollective experience. Thus, it may be that HC constitutes a component of the general recollection network because its activation typically correlates with recollection, but it is not necessary for the conscious experience of recollection. Our findings suggest that HC recruitment supports the factor of context processing, contributing to but dissociable from recollective experience.

The involvement of HC and PHC in context processing is consistent with accounts that emphasize the different kinds of representations carried by MTL subregions (Montaldi & Mayes, 2010; Ranganath, 2010a; Eichenbaum et al., 2007; Davachi, 2006). For instance, the BIC model (Ranganath, 2010a; Eichenbaum et al., 2007) assigns the representation of context information to PHC and the binding of item and context information to HC. Recent work has extended the context processing role of PHC beyond spatial and temporal context to include cognitive context (Diana, Yonelinas, & Ranganath, 2012, 2013; see also Wang, Yonelinas, & Ranganath, 2013), concordant with our findings that PHC is sensitive to reinstatement of semantic context. Our results are less consistent with accounts that suggest a role for the HC in retrieval of information about the attributes of items (e.g., Wixted & Squire, 2011). Even when considering only highly confident recognition hits, presumably associated with "strong"

memories, HC activity was preferentially related to retrieval when the encoding context was reinstated. Although it is possible that the HC may carry some information about items, this information is likely to be integrated with information about the context in which the item was previously encountered (see Hsieh, Gruber, Jenkins, & Ranganath, 2014).

Unlike what was observed in the MTL, activation in the left AnG was sensitive to successful retrieval, independent of context. That is, activity in this region was greater on trials when studied targets were confidently remembered as opposed to forgotten but was not affected by contextual congruency. Neuroimaging studies consistently report activity in posterior parietal cortex (PPC) associated with successful episodic retrieval, a pattern that has been variously attributed to accumulation of mnemonic evidence (Wagner et al., 2005), attention to the contents of memory (Cabeza, 2008), temporary storage of episodic representations (Vilberg & Rugg, 2008), or integration of multimodal episodic details (Shimamura, 2011). When participants' subjective memory reports are assessed, activation peaks are frequently localized to dorsal PPC for familiarity-based recognition and ventral PPC including AnG for recollection-based recognition (Hutchinson, Uncapher, & Wagner, 2009; Spaniol et al., 2009; Vilberg & Rugg, 2008). Whereas the processing of contextual information is one factor that contributes to recollection, AnG activity has also been found to correlate with episodic retrieval even for falsely recognized items (Kahn, 2004; Wheeler & Buckner, 2003), suggesting that it supports the factor of subjective recollection. Moreover, selective deficits in the subjective experience of recollection have been documented in patients with lateral parietal lesions (Simons et al., 2008, 2010; Berryhill et al., 2009; Davidson et al., 2008) and induced in healthy participants via TMS (Yazar et al., submitted). Our findings are consistent with evidence of parietal contributions to retrieval success or recollective experience, independent of context processing.

Within the literature on PPC contributions to episodic memory, a few fMRI studies have examined effects of cue–target congruency. Ciaramelli et al. (2010) adopted this approach to test the Attention-to-Memory hypothesis (Cabeza, 2008), which proposes that attention to the contents of memory involves bottom–up processes, mediated by ventral PPC, and top–down processes, mediated by dorsal PPC. Top–down attentional processes triggered by a relevant or congruent cue would be expected to benefit retrieval of an associated target. Ciaramelli et al. (2010) scanned participants during a cued recognition test for target items from word pairs that were studied at encoding. A significant brain–behavior correlation was found in dorsal PPC for the contrast of targets preceded by studied cues versus no cue, indicating that engagement of top–down attention at retrieval predicted the degree to which congruent cues facilitated target recognition. Park and Rugg (2007) observed similar attentional effects at en-

coding for stimuli that subsequently benefitted from congruent presentation. Participants were scanned as they studied items presented either as words or pictures, then performed a recognition test in which target items were either congruent (same material as encoding, e.g., word–word or picture–picture) or incongruent (different material). Material-independent congruency effects for retrieval success, where activity was greater for subsequently recognized congruent items than incongruent items, were found in dorsal PPC. Although these studies focused on attentional effects governed by dorsal PPC, showing that contextual congruency influences activity in regions supporting top–down attention, this study emphasized memory effects linked to ventral PPC and indicated that AnG recruitment operates independently of context. Our results suggest a role for AnG in translating retrieved information into confident recognition decisions, in contrast to MTL regions, which appear to be more engaged during context reinstatement.

This study collected confidence ratings instead of reports of subjective recollection from participants, an approach that suited the aim of our research but has its limitations. For example, the fMRI analyses evaluated retrieval success with highly confident hits (SureOldHits) contrasted against all misses. Although it is highly likely that many of these items were recollected (Yonelinas, 2001), it is possible that some high-confidence hits were driven by familiarity. Additionally, because of insufficient numbers of trials, it was not possible to separate confidence levels on miss trials. Notably, most models of recognition memory consider guesses (i.e., low-confidence misses) and higher-confidence misses as varying along a continuum of strength of evidence. Thus, there is reason to believe that separating guesses from other misses would not reveal qualitatively different results. Importantly, although mixing no-memory and weak-memory trials in the Misses bin or diluting recollection-based memory decisions in the SureOldHits bin could reduce sensitivity to detect any effects, neither factor would bias our analyses to achieve the predicted result.

In summary, we found widespread main effects of retrieval success within the general recollection network, as expected, but regionally specific activation in HC and PHC for the interaction between retrieval success and the reinstatement of semantic context. Thus, our findings indicate that context processing can be at least partially dissociated from subjective recollection. The pattern in HC and PHC supports our hypothesis based on the encoding specificity principle, as target period activity was greater on trials when the cue word was congruent with encoding context. The context-independent effects of retrieval success in AnG, PCC, and mPFC suggest that these components may implement processes that are more closely related to the subjective experience of remembering. Accordingly, it is likely that the different components of the general recollection network work together, playing different, but complementary, roles in facilitating episodic memory retrieval.

Note

1. To examine whether the results would be affected by restricting the extent of these relatively large ROIs (as compared with smaller MTL subregions), we created 10-mm sphere ROIs around the center of mass coordinates for the AnG, mPFC, and PCC ROIs. ANOVAs using parameter estimates extracted from the spheres replicated the results using full ROIs: The Congruency × Retrieval Success interaction was not significant for any of the parietal or frontal components of the general recollection network (all $Fs < 1$).

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