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Content-Specific Source Encoding in the Human Medial Temporal Lobe

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Although the medial temporal lobe (MTL) is known to be essential for episodic encoding, the contributions of individual MTL subregions remain unclear. Data from recognition memory studies have provided evidence that the hippocampus supports relational encoding important for later episodic recollection, whereas the perirhinal cortex has been linked with encoding that supports later item familiarity. However, extant data also strongly implicate the perirhinal cortex in object processing and encoding, suggesting that perirhinal processes may contribute to later episodic recollection of object source details. To investigate this possibility, encoding activation in MTL subregions was analyzed on the basis of subsequent memory outcome while participants processed novel scenes paired with 1 of 6 repeating objects. Specifically, encoding activation correlating with later successful scene recognition memory was evaluated against that of source recollection for the object paired with the scene during encoding. In contrast to studies reporting a link between perirhinal cortex and item familiarity, it was found that encoding activation in the right perirhinal cortex correlates with successful recollection of the paired object. Furthermore, other MTL subregions also exhibited content-specific source encoding patterns of activation, suggesting that MTL subsequent memory effects are sensitive to stimulus category.

Keywords: fMRI, perirhinal cortex, domain specificity, recollection, medial temporal lobe

It is said that, "A moment lasts all of a second, but the memory lives on forever" (Anonymous). Yet, the landmark case of patient H. M. revealed that new memories only outlast moments if the medial temporal lobe (MTL) is intact. The severe anterograde amnesia that H. M. suffered after bilateral MTL resection revealed the necessity of this region for the formation of new episodic memories (Scoville & Milner, 1957) and has led researchers to explore how the MTL supports episodic encoding. Recent focus is on the relative contributions of distinct MTL subregions, including the hippocampus, perirhinal cortex, and parahippocampal cortex to episodic memory formation (for reviews, see Davachi, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; Mayes, Montaldi, & Migo, 2007; Squire, 2004).

It has been posited that at least two distinct processes support episodic recognition memory: *recollection* and *familiarity* (Jacoby, 1991; Mandler, 1980; Tulving, 1985; for a review, see Yonelinas, 2002). Familiarity has been defined as recognition memory for a given stimulus in the absence of memory for additional episodic details of the initial encounter. Recollection is defined as the recovery of episodic source details surrounding the initial encounter. In a classic example highlighting these two processes, one encounters a person and can recognize that this individual has been previously encountered, but cannot recall any details of the circumstances of that event. This subjective experience, that is, "I know *that* I know you, just not *how* I know you," nicely illustrates the process of familiarity. By contrast, during recollection, one is able to bring back to mind specific episodic source details of the previous encounter, such as spatial and temporal contexts bound to the memory for the individual (Johnson, Hashtroudi, & Lindsay, 1993). The accessibility of these details can drive the subjective memory experience (Johnson & Raye, 1981). Thus, memory quality at retrieval is dependent, at least in part, on binding operations at encoding.

One technique that has widely been used to explore neural encoding operations is the subsequent memory paradigm. Brain data are collected during the study (encoding) phase and later sorted into memory encoding conditions on the basis of each participant's performance on a subsequent memory retrieval test (Paller & Wagner, 2002; Sandquist, Rohrbaugh, Syndulko, & Lindsley, 1980). The nature of the memory test can be altered to allow examination of a number of different forms of memory encoding. For example, one can examine encoding activation correlated with objective measures of recollection through adoption of what have been referred to as source paradigms (e.g., Johnson et al., 1993; Johnson & Raye, 1981). During encoding, study items are presented within experimenter-manipulated contexts that later serve as the *source*, the episodic contextual detail upon which later recollection is assessed. At test, participants are typically asked to make old/new recognition judgments for the item itself and, additionally, to identify the source with which the item was paired during study.

Using this approach, researchers have recently gathered data that have provided evidence that item recognition and source recollection are supported by distinct encoding operations. Specifically, a large body of work has linked hippocampal encoding operations with later recollection and perirhinal encoding with later item recognition (Davachi, Mitchell, & Wagner, 2003; Dou-

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gal, Phelps, & Davachi, 2007; Henson, Rugg, Shalice, Josephs, & Dolan, 1999; Jackson & Schacter, 2004; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Sperling et al., 2003; Uncapher, Otten, & Rugg, 2006; Uncapher & Rugg, 2005). Interestingly, parahippocampal encoding activity has less consistently been associated with either item recognition or recollection. Although many groups report encoding activation correlated with later source recollection (Davachi et al., 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004; Schon, Hasselmo, LoPresti, Tricarico, & Stern, 2004), there is also evidence that parahippocampal encoding activation may correlate with item recognition (Gold et al., 2006; Kirwan & Stark, 2004). Importantly, however, trials for which participants exhibit successful item recognition without source recollection have, in some cases, been treated as trials in which participants only have item familiarity without recollection (for review, see Eichenbaum et al., 2007). It is unknown whether successful item recognition, in some cases, may arise not only from item familiarity but also from recollection of object level details (Staresina & Davachi, 2006).

Although the aforementioned studies provide evidence in favor of differential contributions of MTL subregions to distinct *forms* of memory, other work has shown that MTL regions may differentially contribute to the *content* of memory. Consideration of anatomical inputs to the MTL reveals that perirhinal cortex receives the largest percentage of its input from higher level object processing areas in the ventral visual stream, whereas parahippocampal cortex is the only MTL region that receives input from the spatial processing regions of the dorsal visual stream (Suzuki & Amaral, 1994). This differential cortical input suggests that perirhinal and parahippocampal encoding support might be content specific, that is, differentially important in processing specific types of features or aspects of complex events. Supporting this view, perirhinal cortex has been implicated in the processing of objects, both in tasks that appear primarily perceptual (Buckley, Booth, Rolls, & Gaffan, 2001; Buckley & Gaffan, 2006; Bussey, Saksida, & Murray, 2003; Lee et al., 2005; Litman, Awipi, & Davachi, 2007) and in those that directly measure memory (Kohler, Danckert, Gati, & Menon, 2005; Murray, Bussey, Hampton, & Saksida, 2000; Norman & Eacott, 2005; Pihlajamaki et al., 2004; Staresina & Davachi, 2006). Likewise, a region in posterior parahippocampal cortex has been shown in humans to be differentially sensitive to the spatial relationships inherent in scene stimuli (see Epstein & Kanwisher, 1998) and to items strongly associated with spatial contexts (Aminoff, Gronau, & Bar, 2007; Bar & Aminoff, 2003; Janzen & van Turennout, 2004). Furthermore, two recent animal studies have provided evidence for a double dissociation between anterior and posterior MTL cortical regions, with the perirhinal cortex supporting object memory and the parahippocampal cortex supporting spatial memory (Alvarado & Bachevalier, 2005; Norman & Eacott, 2005). Taken together, these data strongly demonstrate that the MTL cortical regions, including the perirhinal and parahippocampal cortices, are sensitive to particular stimulus categories or event features.

Given this category specificity, it is interesting to note that the majority of memory studies have not systematically manipulated the kinds of event features that have served as study items and those that have served as source details. Although experimentally it is often useful to simplify source to a single, experimenter-controlled dimension, in the real world, source is more complex and can encompass multiple pieces of information (Johnson et al., 1993; Johnson & Raye, 1981). In the example of a chance encounter with a familiar individual, memory for the spatial context of the initial episode could provide source information in support of recollection. Indeed, this situation often prompts the question, “Where do I know you from?” However, spatial context is not the only potentially available source detail. In fact, recollection could be supported by information from many different stimulus categories (see Johnson, Foley, Suengas, & Raye, 1988). A memory of an associated person, (e.g., the individual’s spouse), the presence of a specific object (e.g., cake), or a verbal label (e.g., the individual’s name) bound to the representation of the individual would each provide valuable source information. For this reason, it is important to resist conflating the terms “item” and “source” with specific stimulus categories to prevent misinterpreting differential category effects as differential memory effects (Chalfonte & Johnson, 1996). The source monitoring framework proposes that memories for multiple feature categories can potentially support the experience of remembering, or recollection, when bound in an event (Johnson & Raye, 1981). It follows then that if MTL regions are tuned to respond to different stimulus categories, they may in turn differentially contribute to memory formation through their processing of available event features. Although the encoding effects seen in perirhinal cortex could be interpreted as evidence for a selective role in later familiarity, these findings may simply reflect the fact that, in those studies, item recognition, but not source recollection, was operationalized on recovery of a stimulus that was preferentially processed in the perirhinal cortex. Given that the perirhinal cortex is implicated in object processing, one might speculate that testing *object* source recollection would reveal perirhinal encoding activation consistent with later source recollection.

In the present study, we directly test this hypothesis. During a scanned encoding session, participants are presented with a series of unique scene pictures that serve as study items. Each is paired with one of the six repeating objects that serve as the basis for later source recollection decisions. At retrieval, we first assess old/new recognition memory for each scene. In addition, participants subjectively judge the scenes as “Remember” or “Familiar” to differentiate scene recognition with and without recollection of *scene* details. Each recognized scene (regardless of subjective memory judgment) is immediately followed by a source recollection test in which participants attempt to indicate which object was paired with the scene during study.

Using this design, we find evidence that encoding activation in perirhinal cortex does indeed correlate with later source recollection. Specifically, increased activation was seen in the perirhinal cortex during encoding trials for which the item (scenes) is later recognized, and the correct accompanying source detail (object) is recollected compared with trials for which the item was recognized without object source recollection. This is in contrast to numerous studies reporting perirhinal encoding activation that selectively correlates with item recognition. Interestingly, this object-specific source effect was seen in perirhinal cortex but not in any other MTL region. When participants could not recall the associated object, activation in perirhinal cortex did not differentiate between scenes subjectively rated “Remember” and “Familiar.” Additionally, whereas perirhinal cortex was the only MTL region that showed increased activation specific to object source recollection, parahippocampal cortex and posterior hippocampus appeared to exhibit scene-preferential encoding activation, whereas anterior hippocampus displayed content-general relational encoding.

Method

Participants

Fifteen right-handed, native English speakers participated in the functional magnetic resonance imaging (fMRI) study (6 women). Informed consent was obtained in writing under a protocol approved by the Institutional Review Board of New York University. All participants reported themselves to have normal vision and to be without neurological and psychiatric histories. We removed 2 participants from inclusion in all analyses for insufficient number of trials in which they had correct source recollection (less than 10). Furthermore, we removed an additional 3 participants from region of interest (ROI) analyses because their responses to the Remember/Familiar judgment did not lead to the criterion number of at least 10 trials for all conditions.

Stimuli

During the encoding stage, we presented 192 full color photographs of scenes (96 indoor and 96 outdoor). At test, we presented these studied scenes and a set of 192 novel scenes (96 indoor and 96 outdoor). We culled scene images from various sources, including photo collections (IMSI MasterClips and MasterPhotos Premium Image Collection, San Rafael, CA). The six objects were full color photographs depicting common items (toothbrush, hammer, cup, stapler, cellular phone, shoe). We found these images using an online image search engine (http://images.google.com). For a single participant, each object was paired with 32 different scenes. We counterbalanced the object–scene pairings such that across different participants, each scene was paired with each of the six objects. Scenes were grouped into four sets of 48 scenes that corresponded to each of the functional scans. The presentation order of these sets was also counterbalanced across participants.

Encoding Task

The experiment consisted of an incidental encoding task performed in the magnetic resonance imaging (MRI) scanner, followed by a three-step, unscanned, surprise memory test that assessed the following: (1) scene recognition, (2) subjective recollective assessments for recognized scenes (see below for details), and (3) object source recollection. At encoding, each trial consisted of a 4,750-ms presentation of a composite image that contained a centrally presented novel scene and a smaller image of one of six objects in the upper left corner of the scene image (see Figure 1). For each trial, participants were instructed to imagine using the presented object in the associated scene. Participants were prompted with a response screen to report whether they were successful (two choice) at coming up with a vivid image via a button press on a hand held response box. During the response screen, a green fixation cross appeared (250 ms after the offset of the scene–object stimulus) and remained visible for 1,000 ms. The complete trial duration was 6,000 ms. Trials were presented in a rapid event-related design. In between trials, participants fixated on a white cross. Intertrial fixation intervals ranged from 0 s to 24 s in duration and were jittered according to parameters determined by OptSeq (Dale, 1999). Importantly, trials in which participants were unsuccessful or failed to report success were removed from subsequent analyses. A practice version of the task was administered to each participant outside the scanner to ensure that he or she understood the task and the necessary response timing. Encoding trials were presented across four functional scans that were each 9 min and 36 s long (288 TRs [repetition time; temporal resolution of MRI scans]).

A self-paced memory test was administered on the computer after we removed participants from the scanner (approximately a 20-min study-test interval). During this test, they were presented with all the previously viewed scenes (192 total) and an equal number of novel scenes. Each test trial consisted of presentation of a scene, to which participants were first asked to make an old/new judgment. If they judged a scene old, they were then prompted to

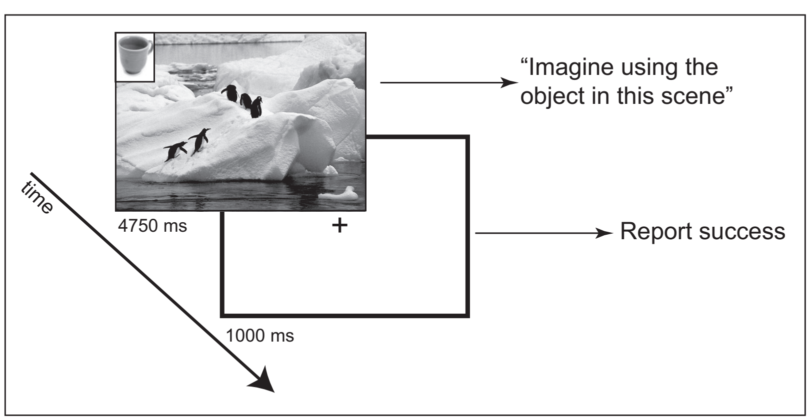

Figure 1. Schematic of a single encoding trial. A full-color, trial-unique scene is presented in the center of the screen with one of six objects, here a cup, presented in the upper left corner of the scene image. This composite image is presented for 4,750 ms. Participants are instructed to imagine using the object in the scene during this time. After a 250-ms pause, a response screen with a green fixation cross appears for 1,000 ms. During this time, participants are instructed to indicate whether they were successful at the encoding task.

judge whether they recollected the scene or whether it was only familiar by labeling scenes "Remember" or "Familiar," respectively (Jacoby, 1991; Mandler, 1980; Tulving, 1985; Yonelinas, 2002). Regardless of this answer, participants were next prompted to either choose the object (out of the six) that was paired with the scene during study or to respond that they did not know (this option was given to minimize guessing). All seven options appeared underneath the scene, labeled numerically (1–7) to indicate the corresponding keystroke. Prior to testing, we provided participants with detailed instructions that explained each judgment that they would have to make, with particular care given to explain the distinction between recollection and familiarity using a clear example to illustrate the two memory conditions. Furthermore, in reference to the specific judgments of the experiment, we provided participants with the following instructions:

> For some of the events, you might recognize the scenes and simply have a feeling of **familiarity** with them, without being able to specifically recollect anything about how they were presented. For other events you might recollect details such as what object was paired with the scene or something else about your previous encounter with the items. This might include remembering the appearance of the picture on the screen, recalling the action you imagined, remembering thoughts you were having or that were triggered by the presentation of the images, and so on. This kind of memory we classify as **recollection** . . . If you make a judgment of **NEW** (press "N"), you will immediately proceed to the next scene. However, if you make a judgment of **OLD** (press "O", you will be asked to indicate whether the scene was familiar, or whether you recollected the scene.

Additionally, we administered a practice test session to ensure that participants understood the test format and the necessary responses.

Imaging Parameters

Imaging data were collected with a 3 Tesla Allegra scanner (Siemens, New York). We acquired functional data across four scans each containing 288 TRs (TR = 2,000 ms; TE [echo time] = 30 ms; flip angle = 80°; 36 slices, 3 × 3 × 3 mm voxels). Slices were coronal and angled perpendicular to the long axis of the hippocampus for optimal coverage of the MTL. A high-resolution, T1-weighted, full-brain, anatomical scan (magnetization-prepared rapid-acquisition gradient echo) was also collected for visualization.

Data Analysis

Behavioral procedures. Trials for which participants failed to report success at the imagery task were removed from further analysis (M = 21%). For the remaining, "successful" encoding trials, we used the results from the recognition memory test to conditionalize the encoding events with regard to subsequent memory. We first binned trials into three main conditions on the basis of memory for components of the initial presentation: miss (M; scene was not recognized), scene only (S; scene was recognized, but the paired object was not correctly identified), and scene and object (S + O; scene was recognized and the paired object was correctly identified). The S condition encompasses both trials with incorrect source judgments and trials in which at the source judgment, participants responded that they "do not remember." This set of conditions allows for objective assessment of memory for an item only (S) compared with memory for an item with additional source information (S + O). It is important to note that in this paradigm, the objective marker of recollection for a trial is memory for the associated object. However, it is possible for participants to have a subjective sense of recollecting the scene itself on the basis of the recovery of scene-based details even without corresponding object source recollection. For this reason, we collected subjective recollection judgments for the scene stimuli for each recognized scene, prior to the assessment of object recollection. Thus, within the S and S + O conditions, we subdivided trials on the basis of the subjective Remember/Familiar scene judgments, creating three conditions: scene only remember (SR), scene only familiar (SF), scene remember and object correctly identified (SR + O). The use of subjective Remember/Familiar ratings allow us to distinguish between object source recollection and recollection driven by other event features. We used these conditions (plus a forgotten items [M or Misses] condition) for subsequent analyses of imaging data. Across participants, there were too few trials for which the object was correctly paired with a scene that was judged familiar (SF + O) to further analyze this condition.

Imaging. For preprocessing and analysis of fMRI data, we used SPM2 (http://www.fil.ion.ucl.ac.uk/spm), a MATLAB-based analysis package (http://www.mathworks.com). We defined ROIs using both anatomical markers and functional activation arising from statistical parametric maps created through linear contrasts of activation during different conditions (see below). We extracted and compared ROI time-course data utilizing the MarsBaR (http://marsbar.sourceforge.net) software package. We performed further statistical analyses using customized MATLAB-based scripts and SPSS (SPSS for Windows, Release 14, 2005; SPSS, Chicago).

Volumes were corrected for different times of slice acquisition, and were realigned correcting for subject movement and scanner drift. Data were next normalized to a Montreal Neurological Institute (Montreal, Canada) reference brain. Data were then smoothed with an isotropic 6-mm full-width half-maximum Gaussian kernel.

We performed data analysis using the general linear model implemented in SPM2. We sorted encoding trials according to the subsequent memory conditions described above, and we modeled them using a canonical hemodynamic response function and its temporal derivative. Participant inclusion in each analysis was dependent on reaching a criterion number of at least 10 trials in each condition being examined. Statistical parametric maps were first computed at the individual participant level. Participant-specific estimates for task-related activation were entered into a second-level random-effects analysis (one-sample t test). Regions consisting of at least five contiguous voxels that exceeded an uncorrected threshold of $p < .001$ were considered reliable.

At the group level, we performed a whole brain linear contrast of task > fixation (N = 13) to identify brain regions engaged during task performance. At the threshold $p < .001$, a large area of the MTL was activated; hence, the significantly activated voxels were spatially contiguous and spanned across the borders of MTL sub-ROIs. To select discrete MTL ROIs, we anatomically constrained the functional voxels emerging from this contrast. First, utilizing MarsBar, we created 6-mm spherical ROIs centered within each MTL subregion according to anatomical markers on the normalized, mean, high-resolution full brain (see Amaral, 1999; Insausti et al., 1998). These anatomical spheres were then used to provide an outline of which voxels emerging from the functional contrast should be included in each MTL subregion. In other words, the overlap of the anatomical and functional data was used to create functional ROIs containing only voxels that showed significant activation during the encoding task but that were also constrained to different anatomical regions (anterior and posterior hippocampus, perirhinal cortex and parahippocampal cortex). It is important to note that although the voxels in these ROIs all showed significantly greater activation compared with fixation during the encoding task, they were unbiased with regard to subsequent memory.

Blood-oxygen-level-dependent (BOLD) activation for the conditions SR + O, SR, SF, and M in different MTL regions was then examined. Data from each ROI were analyzed in a repeated measures design, with planned comparisons made across memory conditions on the peak of the BOLD response ($N = 10$). Percentage of signal change for each condition was calculated against the mean signal of each ROI. For these analyses, we determined the peak in each ROI by averaging across all conditions and participants and determining the point of maximal magnitude of activation. Because the hemodynamic response in MTL regions, particularly hippocampus, may not contain a single clear peak, we characterized the peak response within a region by statistically comparing the numerical peak time point with adjacent time points using a one-tailed t test ($p = .05$). In regions where the numerical peak activation was not significantly greater than that of an adjacent time point, the arithmetic mean of the neighboring time points was used as the peak for within ROI planned comparisons. It is important to point out that whichever peak was used in any given region, the same peak was used for all across-condition comparisons. A separate analysis of variance (ANOVA) was performed specifically to examine interactions across peak activations for the SR + O and SR conditions across selected MTL regions. When across-region comparisons were made, the numerical peak was used for all regions and conditions.

Results

Behavioral

For trials in which participants reported success during study, 54.3% of items (scenes) were correctly recognized, whereas 45.7% were missed or forgotten (see Table 1). The false alarm rate to novel scenes was 5.6%. Comparison of hit and false alarm rates finds significant recognition memory ($p < .001$). Of the correctly recognized scenes, participants correctly recollected the associated object 47.2% of the time, picked the wrong object 22.6% of the time, and chose the “do not remember” option 30.3% of the time.

Analysis of subjective Remember/Familiar judgments for the scenes revealed that 87% of scenes correctly paired with objects (S + O) were also judged remembered, indicating that correctly identified object pairings are strongly indicative of subjective scene recollection as well. However, of the scenes that were recognized without memory for the corresponding object (S), 50.3% were still judged recollected.

Imaging

A contrast of all encoding trials compared with baseline (task > fixation) revealed activation in a large expanse of the MTL, including voxels in right anterior hippocampus, bilateral posterior hippocampus, bilateral perirhinal cortex, and bilateral parahippocampal cortex, as well as extensive activation in bilateral occipital and prefrontal cortices. For the purposes of the present hypotheses, we focus this report on data from within the MTL.

Table 1
Behavioral Data Across Memory Conditions

	Remember		Familiar		Total	
Condition	*M*	*SE*	*M*	*SE*	*M*	*SE*
Scene hits (%)	36.7		17.6		54.3	
Correct source (%)	22.3	3.7	3.3	1.5	25.6	
Incorrect source (%)	9.4	1.6	2.8	0.8	12.3	
No source (%)	5.0	1.5	11.4	2.8	16.4	
Scene miss (%)	NA	NA	NA	NA	45.7	4.1
False alarm (%)	1.5	0.5	4.2	0.9	5.6	

Note. Table shows mean percentages and standard errors of the means across participants for various memory conditions. Conditions reflect subsequent memory for each item or scene as a function of subjective reports of recollection and familiarity. Additionally, within each of those conditions, the proportion of trials for which participants were able to correctly identify object source (object source recollection) is reported such that the following categories apply: correct source = during test, participants select correct object source paired with the item during encoding; incorrect source = participants select incorrect object source; no source = when prompted to select the object source, participants respond “do not remember.”

A critical question was whether perirhinal cortex, a region previously associated with object processing, would show encoding activation consistent with the encoding of source details later supporting recollection. In our paradigm, the objective measure of this would be increased activation for S + O trials compared with S only trials. Consistent with our hypotheses, we found that encoding activation in the right perirhinal cortex ($y = -21$) was significantly greater for S + O trials than that for both S only ($p = .05$) and M ($p = .003$) trials, with S and M trials not significantly differing from each other ($p = .30$; see the top panel of Figure 2B).

Critically, this same pattern was not evident in the parahippocampal cortex. Trials for which the object was later recollected did not differ from those for which the scene only was recognized. The statistical comparisons in the left parahippocampal cortex ($y = -34$) did not reveal any significant differences: S did not differ from S + O ($p = .60$) or from M ($p = .23$), but S + O did show a weak trend toward greater activation compare with M ($p = .13$; see the bottom panel of Figure 2B). These results suggest that the perirhinal cortex was differentially important for encoding object stimuli that serve as the basis for subsequent correct source recollection, whereas the parahippocampal region did not appear to show a similar pattern.

We further probed the differences between conditions for which participants subjectively reported “Remember” or “Familiar” for the individual scenes. We reexamined activation in the same ROIs, now splitting the S + O and S conditions on the basis of these subjective judgments, creating conditions SR + O, SR, and SF. SF + O (familiar scenes with recollected object source) trials were rare and, thus, could not be analyzed.

Importantly, activity in the same right perirhinal ROI continued to show an advantage for encoding object source compared with

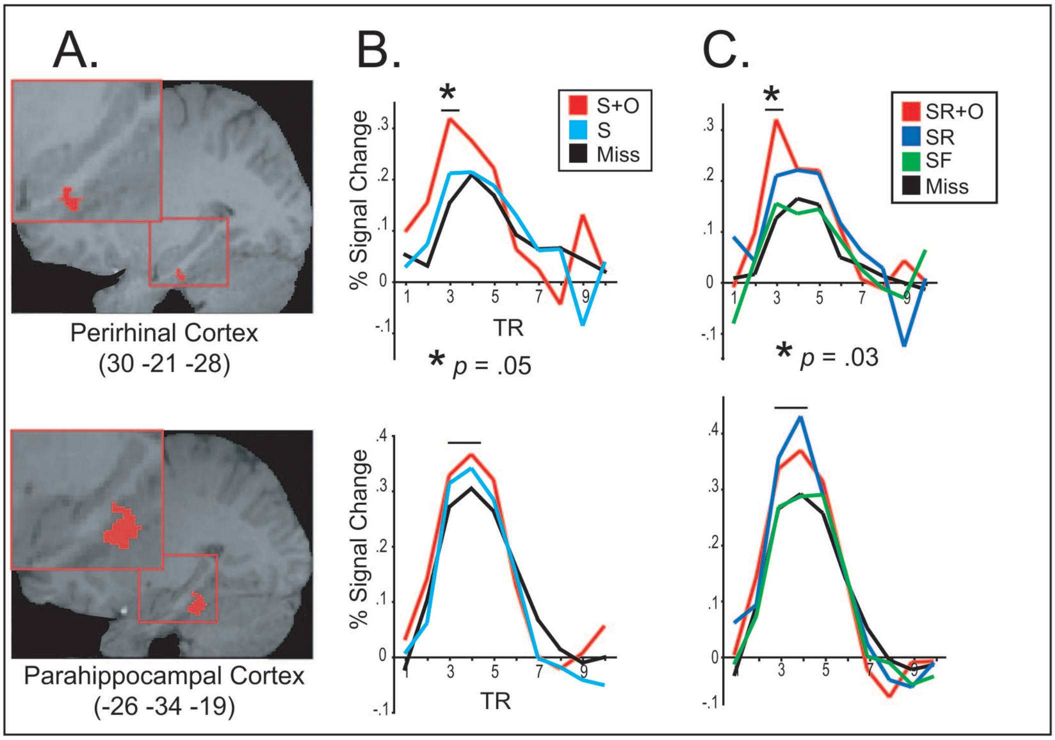

Figure 2. Blood-oxygen-level-dependent responses in cortical regions along the parahippocampal gyrus. (A) Brain regions of interest include the following: top: perirhinal cortex; bottom: parahippocampal cortex. (B) Comparisons of scene and object (S + O), scene only (S), and forgotten items (Miss). In perirhinal cortex, S + O differs from S (p = .05), and no significant differences are seen in parahippocampal cortex. (C) Comparisons in the same regions separating scene memory conditions into those subjectively reported as "Remember" (recollected) or "Familiar." In perirhinal cortex, scene remember and object correctly identified (SR + O) is significantly greater than scene only remember (SR), despite the fact that both scenes are judged remembered. This trend appears inverted in parahippocampal cortex, with SR numerically greater than SR + O. SF = scene only familiar; TR = repetition time in magnetic resonance imaging scans.

encoding of the scene only, even when the scene was judged remembered (see the top panel of Figure 2C). Specifically, significantly greater activation was seen for SR + O trials compared with all other trial types—SR (p = .03), SF (p = .001), and M (p = .0001)—indicating increased encoding activation during trials for which the object source details were later recollected compared with when scene details were later recollected. Moreover, SR did not differ significantly from either SF (p = .30) or M (p = .10), further suggesting that the perirhinal cortex does not support all forms of later recollection.

A similar analysis in the left parahippocampal ROI revealed a different pattern across these memory conditions. Activation was numerically greatest during trials with scenes recollected without the associated object source. Although comparison of SR activation with that of SR + O did not reach statistical significance (p = .30), SR activation was significantly greater than that of SF (p = .02) and M (p = .007; see the bottom panel of Figure 2C). Additionally, in the parahippocampal ROI, SR + O also differed from M (p = .04; see the bottom panel of Figure 2C). Interestingly, in contrast to the perirhinal region, this parahippocampal region showed numerically less activation during trials when object source details were subsequently recollected compared with when only scene details were remembered, suggesting that the encoding of different source attributes is distributed across the MTL cortex.

Analyses of hippocampal regions also revealed interesting dissociations (see Figure 3A). On the one hand, anterior hippocampus exhibited similar activation levels for all trials later recollected, regardless of the episodic content supporting recollection. On the other hand, posterior hippocampus showed a benefit for scenes recollected without object source details compared with those recollected with object information, similar to the pattern seen in posterior parahippocampal cortex. Specifically, in right anterior hippocampus ($y = -10$), encoding activation for the SR condition was significantly greater than that for M (p = .02); this was paralleled with SR + O trending toward being greater than M (p = .099). Here, SR + O and SR did not significantly differ from each other (p = .48). By contrast, in right posterior hippocampus ($y = -31$), SR activation was significantly greater than SR + O (p = .002), M (p = .004), and SF (p = .02). SR + O did not differ significantly from SF (p = .40) or M (p = .20; see Figure 3B).

Together, the results from both hippocampus and neocortical MTL regions perirhinal and parahippocampal cortices suggest distinctions along the anterior–posterior axis of the MTL. To statistically examine these distinctions, we performed two-way

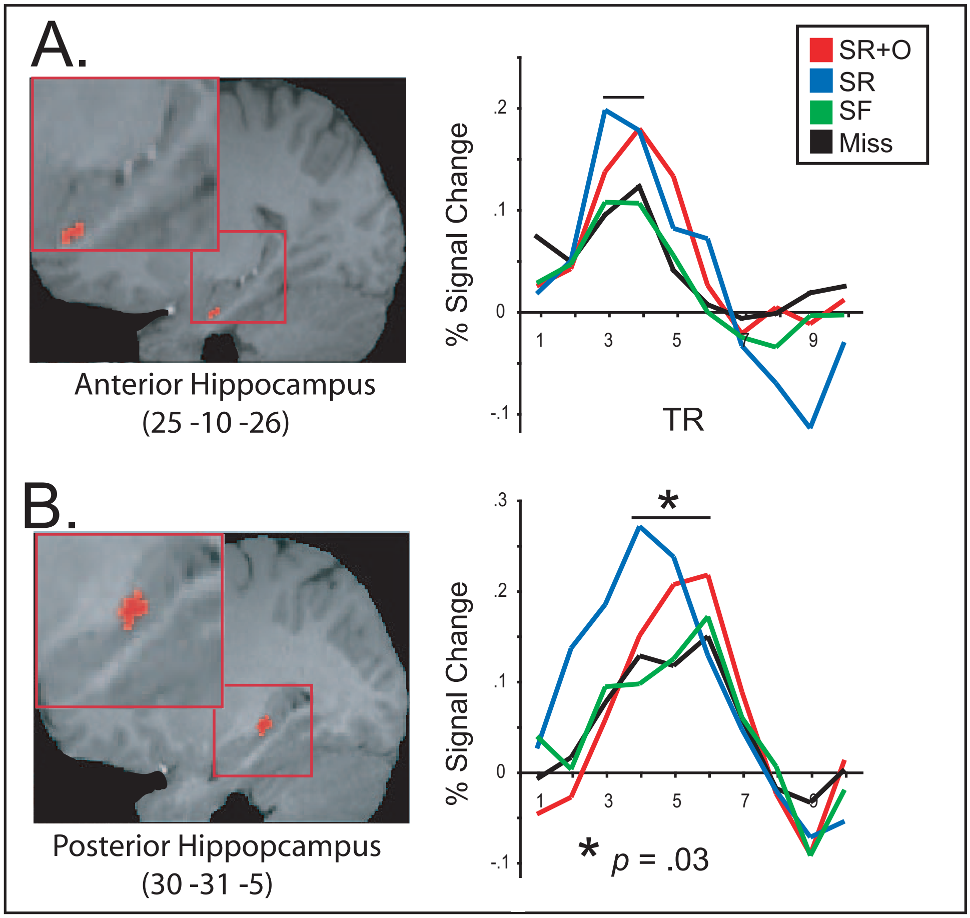

Figure 3. Blood-oxygen-level-dependent responses in hippocampus. Plots show hemodynamic responses for four conditions (scene remember and object correctly identified [SR + O], scene only remember [SR], scene only familiar [SF], and forgotten items [Miss]). (A) Region of interest (ROI) in anterior hippocampus shows comparable activation for SR and SR + O, suggesting content-general recollective effects. (B) ROI in posterior hippocampus: SR shows significantly greater activation compared with all other conditions, including SR + O. TR = repetition time in magnetic resonance imaging scans.

repeated measures ANOVAs with the factors Region (perirhinal and parahippocampal cortices) and Content of recollection (SR + O, SR) to assess differences between responses during SR + O and SR conditions across these MTL regions (see Figure 4A). We found a main effect of Region, $F(1, 9) = 5.607$, $p = .04$, but not of Content, $F(1, 9) = 0.286$, $p = .60$. Importantly, a significant interaction between Region and Content, $F(1, 9) = 8.139$, $p = .02$, was seen, highlighting that perirhinal activation was greater when objects were later recollected, whereas parahippocampal activation was greater when scenes were later recollected.

A similar two-way ANOVA was conducted for the hippocampal regions with Region (anterior and posterior hippocampus) and Content (SR + O, SR) as factors (see Figure 4B). There were no main effects of Region, $F(1, 9) = 0.540$, $p = .50$, or of Content, $F(1, 9) = 3.36$, $p = .10$. However, a marginal interaction was seen, $F(1, 9) = 4.44$, $p = .06$, driven by the result that activation in anterior hippocampus was not differentiated by memory content, whereas activity in posterior hippocampus was less for scenes recollected with associated object source compared with scenes recollected without.

Discussion

The present study provides evidence for distinct patterns of encoding activation in MTL subregions related to the type of event content later recollected. Our design enabled identification of three different subsequent memory components for each individual encoding trial: (1) old/new recognition memory for scenes, (2) participant's subjective recollective experience for recognized scenes ("Remember" or "Familiar"), and (3) object source recollection, or remembering which of six objects were paired with the scene during encoding. Comparison of the encoding activation linked to these mnemonic measures revealed that activation in parahippocampal cortex and posterior hippocampus correlated best with scene encoding, whereas activation in right perirhinal cortex was greatest when the presented object was successfully bound to the scene stimulus. Furthermore, a region in the right anterior hippocampus exhibited activation that, consistent with a content-general relational binding mechanism, did not differentiate between the different stimulus categories of recollected content. Taken together, these results provide evidence for content-

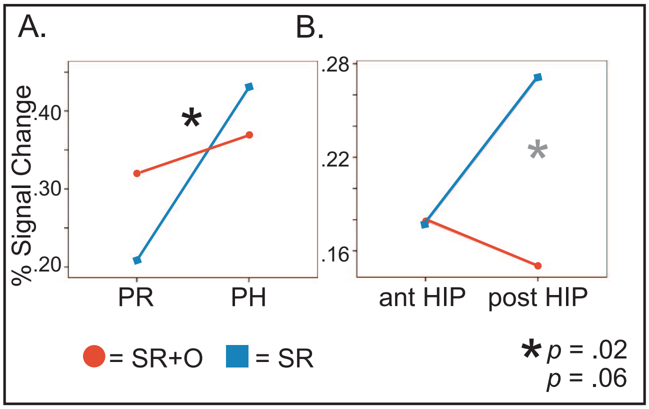

Figure 4. Region × Condition interactions. Activation for scene remember and object correctly identified (SR + O) and scene only remember (SR) conditions that differed on subsequent object source recollection were compared across different medial temporal lobe regions. (A) Comparison of perirhinal cortex (PR) and parahippocampal cortex (PH) reveals a significant Region × Content interaction for SR + O and SR across the anterior (ant) PR region and in the posterior (post) PH region. (B) Comparison of the same conditions in ant hippocampus (HIP) and post HIP reveals an interaction that trends toward significance ($p = .06$).

dependent distinctions between the contributions of perirhinal and parahippocampal cortices to source encoding and also suggest important divergent contributions of different hippocampal regions to binding operations.

Data from single unit and human functional imaging experiments have suggested that perirhinal operations are selectively important for item, but not source, or relational encoding (Davachi et al., 2003; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Uncapher et al., 2006; for review, see also Brown & Aggleton, 2001). In the majority of paradigms used, however, researchers have predominately indexed source recollection using memory for a spatial or cognitive context (Davachi et al., 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004; Uncapher et al., 2006; but see Kirwan & Stark, 2004). In the current experiment, we indexed recollection on successful source memory for a previously presented object in each event as well as on subjective measures of scene recollection. In this case, perirhinal activation showed a pattern consistent with successful object source encoding, that is, when objects were bound to scenes. Specifically, activation in right perirhinal was greater during encoding of scenes later recollected with the presented object (SR + O) than when scenes were recollected but the presented objects were not (SR). Furthermore, perirhinal activation did not statistically differentiate between scenes later judged recollected (SR) and scenes subsequently judged familiar (SF) or forgotten (M). Finally, this object-selective pattern of activation was seen only in right perirhinal cortex; no other MTL-examined region showed this effect.

It is important to note this finding in and of itself is not inconsistent with the notion that perirhinal mechanisms are important in encoding processes that support later familiarity. Indeed, from that perspective, the enhancement from the SR condition to the SR + O condition may be seen because the SR + O condition elicits, on average, greater subsequent episodic familiarity. However, as stated above, the pattern seen across the other memory conditions is not consistent with the notion that MTL cortex solely supports later gradations in familiarity that are independent from stimulus content. Specifically, the lack of a graded effect from SR to SF, and from SF to M, argues against a general familiarity mechanism. Instead, the overall pattern suggests that perirhinal encoding processes are important for object encoding and, hence, may contribute to not only familiarity but also to recollection of object details. Recently, a few studies have also reported findings broadly consistent with this notion, showing that perirhinal encoding activation correlates with intra-item associative binding (Staresina & Davachi, 2006, 2008; Tendolkar et al., 2007) but not item-context binding (Staresina & Davachi, 2008). Furthermore, these data are in accord with cognitive models (e.g., Johnson et al., 1993) and models of MTL organization that explicitly take episodic content into account (Davachi, 2006; Mayes et al., 2007).

One critical consideration is whether the increased activation seen in perirhinal cortex is sufficient to support later recollection. We think this is unlikely given overwhelming evidence that patients with selective hippocampal damage appear to be grossly impaired in recollecting specific features of events (Manns, Hopkins, Reed, Kitchener, & Squire, 2003; Wixted & Squire, 2004; Yonelinas, 2002). Instead, we propose that perirhinal processes may be important in item encoding both in the service of later familiarity and, perhaps in concert with hippocampal operations, in the service of binding object features in support of later recollection. It remains to be seen to what extent perirhinal and hippocampal encoding operations cooperate or act independently during episodic encoding.

Further examination is needed to address whether the enhanced activity in right perirhinal could be a direct consequence of low-level operations, such as foveation on the presented object, which may also be related to memory encoding. According to this account, the correlation between perirhinal BOLD activation and object source recollection may be indirect and mediated by a direct relationship between perirhinal activation and object viewing, which may also relate, albeit indirectly, to later memory. Specifically, it is possible that differential foveation on the presented object across trials may modulate perirhinal activation and that longer foveation trials are also trials for which participants are more likely to later remember the paired object. Inherent in this account is the assumption that perirhinal cortex is sensitive to the mere presence of a stimulus in the visual world of the observer. There is evidence that perirhinal neurons show stimulus specificity for objects (Miller, Li, & Desimone, 1991; Sakai & Miyashita, 1991), and although much lesion work supports the notion that perception is intact with MTL damage (Buffalo, Reber, & Squire, 1998; Hampton & Murray, 2002; Holdstock et al., 2000), a series of recent studies have proposed that perirhinal cortex may be critical for object perception (Buckley et al., 2001; Buckley & Gaffan, 2006; Bussey & Saksida, 2002, Bussey et al., 2003; Eacott & Gaffan, 2005). However, much of the neuropsychological work linking perirhinal cortical damage with perceptual deficits includes patients who, in addition to perirhinal damage, also have measurable lateral temporal damage, greatly limiting what can be concluded about perirhinal cortex and perception from those studies (Shrager, Gold, Hopkins, & Squire, 2006). Additionally, it has been posited that the perceptual tasks used in these experiments are themselves dependent on learning and memory (Hampton, 2005).

Nonetheless, it will be important for future studies to closely monitor viewing behavior to examine this possibility.

In contrast with the perirhinal cortex, which did not exhibit a pattern consistent with scene encoding, parahippocampal cortex and posterior hippocampus showed significantly greater activation for scenes reported as being subjectively recollected compared with those reported as simply familiar. Interestingly, parahippocampal cortex and posterior hippocampus actually showed less activation when object information was accurately recollected compared with when the scene was recollected alone. The decreased activation in these regions when it would appear that more information was being encoded (SR + O) leads us to speculate that successful binding of the scene with the object may have reduced the attentional resources available to bind other features, such as those within scenes or between scenes and participants' preexisting experiences. In any event, this pattern of results suggests the possibility that no single MTL brain region should be used as an indicator of how much information is being encoded. Instead, these data suggest that the pattern across MTL regions may be a better measure of memory content. Although the exact mechanisms behind such a pattern are unknown, one possibility is that during any given event, attentional resources are limited; hence, gating of these resources leads to differential activation distributed across MTL brain regions depending on the target(s) of attentional focus. In terms of the present data, if perirhinal and parahippocampal cortices differentially support the encoding of objects and scenes, respectively, the BOLD data might reflect the *sum of activation* volleying between the two regions and, hence, may also correlate with the overall content of the subsequent memory as we see in our data. Another factor that could contribute to such a pattern is that the SR condition may not reflect a condition in which there is overall less source detail recollected than in the SR + O condition but rather one in which *qualitatively different* source detail is recollected. Although participants are explicitly tested on source recollection for the presented object, presumably other, nonexperimenter manipulated source details can drive "Remember" judgments (e.g., Johnson et al., 1988). Thus, the two "Remember" conditions may not necessarily reflect a difference in the amount of recollected detail but the content.

We also found that activation along the hippocampal anterior–posterior axis yields both similarities and differences. One similarity between the anterior and posterior hippocampus is that both regions displayed increased encoding activation for subsequently recollected scenes compared with those that were later judged familiar or new, replicating prior studies showing a strong correlation between the hippocampus and relational binding (Chua, Schacter, Rand-Giovannetti, & Sperling, 2007; Davachi et al., 2003; Dougal et al., 2007; Henson et al., 1999; Jackson & Schacter, 2004; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Prince, Daselaar, & Cabeza, 2005; Ranganath et al., 2004; Sperling et al., 2003; Staresina & Davachi, 2006, 2008; Uncapher et al., 2006; Uncapher & Rugg, 2005; see also Cohen & Eichenbaum, 1993) but contrasting with work suggesting that anterior, but not posterior, hippocampus relational processes differentially contribute to subsequent memory (Chua et al., 2007). Interestingly, consideration of stimulus category yields a potential dissociation in the current data. Anterior hippocampus displayed activation consistent with a content-general relational binding process with a similar magnitude of encoding activation for recollected scenes regardless of correct object source identification. Consistent with this, other recent reports have provided evidence for content-general relational encoding and retrieval in anterior hippocampus (Prince et al., 2005) as well as have shown evidence that anterior hippocampus appears to distinguish between the amount of source information subsequently recollected rather than the type (Staresina & Davachi, 2008). By contrast, posterior hippocampus appears preferentially responsive to the encoding of the scene stimuli as discussed above. In right posterior hippocampus, scenes recollected without the object source showed greater activation than all other memory conditions, including recollected scenes that also included object source information. These findings are redolent of evidence suggesting posterior hippocampus may be preferentially engaged in spatial processing (Moser & Moser, 1998; Pihlajamaki et al., 2004). Although further work will focus on understanding the functional architecture of the hippocampus, extant data in the rodent suggest that parahippocampal–hippocampal inputs preferentially project to the dorsal hippocampus (Hargreaves, Rao, Lee, & Knierim, 2005), a region thought to correspond to posterior hippocampus in humans. Thus, one can speculate that posterior hippocampus mechanisms may be operating on input from spatial information processing parahippocampal regions, rendering them more sensitive to spatial information encoding. However, this same logic cannot simply explain the anterior hippocampus effects that did not show any preferential encoding effects on the basis of event content but instead appeared selective to memory quality only.

In conclusion, these data shed light on the differential role of MTL cortical regions in object and scene encoding and provide initial evidence for an anterior–posterior distinction along the hippocampus. More broadly, however, the current results support the notion that episodic memory quality is derived from differential processing of specific source features (e.g., Johnson et al., 1993) and that such content is an important organizing principle of the MTL (Davachi, 2006). Given this, it follows that all differential encoding activation patterns across MTL subregions seen in previous studies (Davachi et al., 2003; Henson et al., 1999; Jackson & Schacter, 2004; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Staresina & Davachi, 2006; Uncapher et al., 2006; Uncapher & Rugg, 2005) are likely influenced by the categories of stimuli used in those paradigms. Hence, consideration of potential stimulus category effects should inform future studies of episodic encoding.

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