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Parahippocampal cortex activation during context reinstatement predicts item recollection

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Abstract

Episodic memory is the binding of an event with information about the context in which that event (or item) was experienced. The context of an event may include its spatial and temporal location as well as goal-directed, conscious thoughts evoked during the event. We call this latter type of information "cognitive context." The Binding of Items and Context (BIC) theory of medial temporal lobe function proposes that parahippocampal cortex (PHc) plays a key role in processing cognitive context. Therefore, we predicted that activity in PHc during reactivation of a previously experienced cognitive context would be correlated with item recollection, even when the associated item and its episodic binding had not yet been retrieved. Using a novel paradigm, we measured brain activation with fMRI in response to covert reinstatement of a cognitive context, prior to presenting an item memory probe. Contexts were studied with multiple items to ensure that spontaneous item retrieval would not occur prior to the test probe. At test, contexts were reinstated for eight seconds before the test probe was presented. We manipulated whether the reinstated context matched the encoding context of the test probe that followed. For such matching contexts, we found that increased PHc activation prior to the test probe predicted recollection following the test probe. If a context unrelated to the eventual test item probe was reinstated, there was no such association between PHc activation during context reinstatement and eventual memory judgments. These findings suggest that PHc activation is correlated with cognitive context retrieval.

Keywords

context reinstatement; parahippocampal cortex; recollection; fMRI; hippocampus

Episodic memory was first defined by Tulving (1972) as encoding and retrieval of an event, including information about how that event is associated with other memories. Four decades after Tulving's foundational theory was published, episodic memory is a well-accepted concept though modern definitions of episodic memory have expanded upon the original theory. Tulving's description of the secondary information that is retrieved along with an event has been refined and is now more typically labeled "context." Process theories now typically include a second, related, retrieval mechanism that does not require context retrieval but that allows judgments about the recency of an event. This process is called "familiarity," whereas Tulving's originally proposed retrieval process is called

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"recollection." In general there is widespread agreement upon the idea that the context of an episodic memory includes spatial and temporal details.

In addition to temporal and spatial information, context may also include internally generated information, such as goal-directed thoughts evoked by the item at the focus of attention, which we will call "cognitive context." Participants' idiosyncratic associations or elaborations that come to mind during encoding of an item can be a salient marker of the study event. This phenomenon was also originally described by Tulving and termed "subjective organization" (1962). For example, one participant studying the word "fish" may associate that item with his pet goldfish while another participant may associate that item with plans to have salmon for dinner. These associations may then be retrieved at test when the target item is cued. In our example, the test cue "fish" may trigger the first participant to recall his thoughts about his pet goldfish and therefore recollect the encoding event. The current experiment investigates the role of such cognitive context in episodic memory retrieval. In particular, can cognitive context reinstatement prime recollection of an event? If so, what brain regions are associated with reinstatement of cognitive context, and does activation in these regions predict recollection of the binding between an item and that context?

Patient studies have demonstrated that the medial temporal lobe (MTL) is the primary brain region necessary for encoding episodic memories. Damage to the hippocampus results in particularly profound anterograde amnesia (Corkin, 2008; Scoville & Milner, 1957). As with any brain region, the function of the hippocampus relies on inputs from other areas of the brain. The hippocampus receives the majority of its input from entorhinal cortex. Entorhinal cortex, in turn, receives inputs from both parahippocampal cortex (PHc) and perirhinal cortex (PRc) (Eichenbaum, Yonelinas, & Ranganath, 2007). Episodic memory research in recent years has therefore turned to investigating PHc and PRc in order to understand the nature of inputs to the hippocampus and give insight into the transformation of those inputs during hippocampal processing. The function of PHc is particularly mysterious, and an increasingly large body of empirical findings and theories are focused on uncovering its unique function in episodic memory (e.g. Aggleton & Brown, 2006; Brown & Aggleton, 2001; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum et al., 2007; Epstein & Kanwisher, 1998; Graham, Barense, & Lee, 2010; Kirwan, Wixted, & Squire, 2008; Suzuki, Tsukiura, Matsue, Yamadori, & Fujii, 2005).

The Binding of Item and Context (BIC) theory of MTL subregion function proposes that MTL subregions are differentially involved in processing the types of information that form the components of an episodic memory. This theory is derived in part from neuroimaging studies examining the neural correlates of source recognition, which have shown that activity in the hippocampus and PHc is associated with memory for context information (Davachi, Mitchell, & Wagner, 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004). In contrast, activity in PRc is associated with strength-based item recognition but not with context retrieval (Davachi et al., 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004; Uncapher, Otten, & Rugg, 2006; Weis et al., 2004). Therefore, the BIC theory proposes that PHc processes context information and PRc processes item-specific information. The hippocampus, given its specialized anatomical properties and position in the MTL information stream, is thought to bind these pieces of information into a coherent representation of the event in context. Recent evidence from an adaptation study supports a dissociation between the roles of PRc and PHc during item encoding (Diana et al., 2012). Adaptation paradigms measure the reduction in fMRI activation due to repetition of an

[1]It should be noted that these results are consistent with both dual process theories (Aggleton & Brown, 2006; Diana, Reder, Arndt, & Park, 2006; Yonelinas, 2002) and the BIC theory.

event. Repetition of item information (an object picture) was associated with adaptation in PRc whereas repetition of context information (a distinctive study question) was associated with adaptation in PHc.

Further information about the relationship between MTL subregion function and the components of episodic memory can be gained through context reinstatement paradigms. In context reinstatement, peripheral details from the study event are presented at test to facilitate recollection of the association between an item and that context. This paradigm is a modification of the typical recognition memory task in which participants are given an item cue alone and asked to retrieve the relevant context. In everyday life the typical recognition memory task is akin to seeing a person (item) and retrieving the time or place where you met that person (context). A parallel example of a context reinstatement paradigm might be leaving your office (context) and encountering a familiar person (item). The recent priming of your office might contribute to recollection of having first met that person during your office hours.

Bar, Aminoff, and colleagues have addressed the concept of context reinstatement in a series of studies within the perceptual domain. These studies have made use of visual images that call to mind a particular visual context (“strong context objects”, e.g. a traffic light) as compared to images that are not associated with a specific context (“weak context objects”, e.g. a laptop). Several experiments have found PHc activation during processing of strong context objects but not weak context objects (Aminoff, Gronau, & Bar, 2007; Bar & Aminoff, 2003; Bar, Aminoff, & Ishai, 200; Bar, Aminoff, & Schacter, 2008). In addition, perception of strong context objects has been found to induce neural synchrony in PHc as early as 150 ms after stimulus onset (Kveraga, et al., 2011). This finding suggests that the process of recalling a relevant context during object perception facilitates object recognition. The early onset of synchrony indicates that context is reinstated almost immediately after object perception. Reinstated visual context may serve as an episodic memory cue as well as an object recognition cue, but this question has not been previously studied.

Prior research demonstrates that memory performance is higher when the cognitive state and physical details experienced during encoding are reinstated during retrieval (McDaniel, Robinson-Riegler, & Einstein, 1998; McGann, Ellis, & Milne, 2002; Nowinski & Dismukes, 2005). Consistent with this behavioral finding, neuroimaging studies have demonstrated that the overall pattern of activation in the brain during successful recollection reflects the encoding task that was assigned to the recollected item (Gilbert, Armbruster, & Panagiotidi, 2012; Johnson et al., 2009). This effect was obtained even in studies that examined modality-specific brain regions as opposed to the brain as a whole (Johnson et al., 2009; Johnson & Rugg, 2007; Polyn, Natu, Cohen, & Norman, 2005; Rugg, Johnson, Park, & Uncapher, 2008). For example, when faces and scenes were paired during encoding, a single retrieval cue from either category produced activation related to both faces and scenes in modality-specific areas (Hofstetter, Achaibou, & Vuilleumier, 2012). This suggests that a partial cue for an event results in reinstatement, and perhaps mental imagery, of event details that are not included in the cue.

The studies described above indicate spontaneous reactivation of encoded information during encoding and retrieval. However, as concluded by Gilbert and colleagues (2012), these studies cannot distinguish between two possible interpretations of their results. Does reactivation of the context representation contribute an ongoing recollection process? Or does reactivation of the context representation indicate a completed recollection process?

Many studies have already found that MTL activation is a marker of recollection (e.g. Davachi et al., 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004). Therefore, the

"correlation" explanation of context reinstatement simply adds modality-specific brain regions to the list of areas activated by recollection. The former explanation would provide exciting insight into the relationship between item and context information at retrieval. In addition, if MTL subregions are involved in triggering recollection based on reactivation of encoding information, this finding may restrict the range of possible theories of MTL subregion function. To our knowledge, no studies have demonstrated reactivation of the brain state at the time of encoding acting as a trigger for recollection of an item. The current study was designed to answer this critical question using a novel paradigm in which fMRI activation due to context reinstatement could be measured in the absence of item recollection. This paradigm also allowed us to link activation during the context reinstatement period to item recollection success during a later time period. We began this investigation with specific predictions for MTL subregion activity that were derived from the BIC theory.

One of the key ideas in the BIC theory is that PHc is the critical region for processing context information. An untested prediction based on this idea is that reinstatement of context information, in this case cognitive context, should be reflected in PHc activation. In addition, activation of context representations in PHc should predict recollection of an associated item but not familiarity-based retrieval of that item. If these predictions are correct, we should find that reinstatement of an encoding context modulates PHc activity such that it serves as a predictor of recollection *prior to revealing the tested item*.

We manipulated cognitive context using distinctive encoding questions which were designed to induce a personal and idiosyncratic mental state for each participant while encoding a series of words. During an item test of the studied words, with recollection and familiarity judgments, we used a cover task to covertly reinstate the encoding questions. The item probe on each test trial was not presented until after context reinstatement. The cover task was intended to prevent subjects from adopting a retrieval strategy based on the context reinstatement portion of the trial. In addition, we presented eight individual words with each encoding question during the study list in order to minimize spontaneous item retrieval during the reinstated context. The encoding question presented during the cover task was relevant to the test probe on 33% of the trials. That is, the reinstated context was either the encoding question originally used to study the test item or an encoding question used to study a different test item. This allowed us to attribute pretest PHc activation to reinstatement of a particular context rather than a cognitive state that was favorable for recollection in general. We analyzed fMRI activation during reinstatement of the encoding question but before presenting the item cue in order to assess whether pre-test PHc activation predicted later item recollection.

Materials and Methods

Participants were 19 right-handed adults from the University of California, Davis community ranging in age from 18 to 29, with a mean age of 20. Six participants were male. Word stimuli for the experiment were randomly drawn from a pool of 994 nouns (collected from the MRC database, Coltheart, 1981) with four to ten letters, average concreteness of 585, and average Kucera-Francis frequency of 36.4. Encoding questions were randomly drawn from a pool of 156 experimenter-created yes/no questions (e.g. "Could this item melt?" see Figure 1) that require processing of the conceptual features of each item (also used in Diana et al., 2012).

The study portion of the experiment was completed outside the MRI scanner. Study words were presented with an encoding question for 4 seconds each. Participants were asked to read the word and respond to the yes/no question in terms of the given word. Encoding

questions were randomly assigned to words with a total of eight words being presented with each question across the study list. Thus, there was not a one-to-one mapping between the studied items and the encoding question. Participants were given explicit instructions that their goal was to remember the words. They were told that the questions were designed to help them process the words in unusual ways and thus improve their memory for the words.

MRI images were recorded during a test of item memory that was divided into 6 runs of 36 trials each, for a total of 216 retrieval trials. Figure 1 shows sample test trials for each condition including the trial timing. During a 4-second sham "study" period at the beginning of each trial, a new word was presented with one of the previously studied encoding questions and participants were asked to respond yes or no to the question. Participants were told that the purpose of this new study trial was to investigate the effect of studying new information on their memory for previously learned information. The actual purpose of this portion was to reinstate an encoding question that was originally studied with the subsequent test probe (Match condition) or that was originally studied with different test items (Mismatch condition). This sham "study" portion was followed by a 4-second delay period. These two portions of the trial (8-seconds in total) will be referred to as the "pretrial cue period." Next, the test probe was presented on-screen for 2 seconds followed by a 2-second fixation. This 4-second portion of the trial will be referred to as the "test probe period." The last portion of each trial was a variable intertrial interval with a mean length of four seconds. The length of each intertrial interval was determined by an optimization simulation using the optseq program (http://surfer.nmr.mgh.harvard.edu/optseq/). We used an active baseline in which participants viewed single digits during the intertrial interval and were asked to respond "odd" or "even," using a key press, with a new digit appearing every 2 seconds. These odd/even judgments were intended to prevent mind wandering, which might result in increased MTL activity during the baseline period.

We collected Remember/Know/New judgments (Tulving, 1985) during the test portion of the experiment. Participants were asked to respond "Remember" if they experienced recollection and were able retrieve details about the experience of studying the test word during the trials outside of the scanner. They were specifically instructed that remembering the question used to study the word should result in a Remember response. Participants were asked to respond "Know" if the word seemed familiar such that it was likely to have been studied in the experiment, but only when they could not retrieve any details about the experience of studying the test word. Know responses serve as a measure of familiarity. New judgments indicated a word that the participant did not remember appearing on the study list. The tests included a total of 72 old words in the Match condition, 72 old words in the Mismatch condition, and 72 new words. The Match, Mismatch, and New test probes were all preceded by pretrial cue periods that were identical in procedure.

MRI data were acquired at the University of California, Davis Imaging Research Center using a 3T Siemens Trio scanner equipped with a 32-channel phased array head coil. Pre-screening interviews ensured safety in the scanner, and earplugs were provided to attenuate acoustic noise from the scanner. Padding and adjustable head restraints were used to minimize head motion. Functional data were obtained with a gradient echoplanar imaging (EPI) sequence (repetition time/TR, 2000 ms; echo time/TE, 25 ms; field of view, 220); each volume consisted of 36 axial slices, with a thickness of 3.4 mm and no interslice gap, resulting in a voxel size of 3.4×3.4×3.4 mm. Additionally, T1-weighted images coplanar with the EPIs were acquired using an MPRAGE sequence (field of view, 243; voxel size = 1×1×1mm, number of slices = 192). Preprocessing was performed using Statistical Parametric Mapping (SPM8) software. EPI data were slice-time corrected with sinc interpolation to account for timing differences in acquisition of adjacent slices. The data were then realigned using a six-parameter, rigid-body transformation. Following

realignment, the high-resolution structural image for each participant was co-registered to the mean EPI image for that participant. The unified segmentation tool in SPM8 was then run on the high-resolution structural image to calculate normalization parameters for each participant. The normalization parameters calculated during segmentation were applied to the EPI images, which were then resliced into 3mm isotropic voxels. Finally, the images were spatially smoothed with an 8 mm full-width at half-maximum Gaussian filter.

We conducted separate GLM analyses of the fMRI data from the pretrial cue period and the test probe period using SPM8. Outliers were identified in the data using the Artifact Detection Tools (ART, http://gablab.mit.edu/index.php/software) in SPM8 with thresholds for global signal intensity (z = 10), translational movement (1 mm), and rotational movement (0.1 rad). The outlier TRs were then modeled as covariates of no interest. We used a square wave (convolved with the hemodynamic response function)to model the complete interval of each relevant trial portion. The pretrial cue period analysis was modeled as the 8 seconds following the sham "study" trial and prior to test probe onset. The test probe period was modeled as the 4 seconds between test probe onset and the beginning of the active baseline. Cluster thresholds were determined by Monte Carlo simulations, as implemented in the 3dClustSim program in the AFNI software package (Cox, 1996). The simulations were based on anatomical masks of areas with *a priori* predictions. For the MTL mask, we used a minimum cluster size of 13 combined with a threshold of $p < .005$ to result in a mapwise false-positive rate of $p < .05$. For the PHc mask, we used a minimum cluster size of 22 combined with a threshold of $p < .05$ to result in a mapwise false-positive rate of $p < .05$. Whole brain analyses, for which we had no *a priori* predictions, were based on a minimum cluster size of 79, combined with a threshold of $p< .005$, to result in a mapwise false-positive rate of $p < .05$.

Results

Behavioral Analyses

The Match condition produced more Remember hits ($M = 60.2\%$) and a larger overall d′ ($M = 0.84$) than did the Mismatch condition ($M = 57.6\%$, $M = 0.80$), however this difference was not statistically significant, $t(18) = 1.80$, $p = 0.09$ and $t(18) = 1.91$, $p = 0.07$, respectively. Data from a separate behavioral study, which included 32 new participants tested with the same procedure and stimuli, replicated the pattern of results from the fMRI study (see Figure 2). With this larger sample size, the differences in Remember hits and d′ for the Match condition ($M = 63.3\%$, $M = 0.91$) as compared to the Mismatch condition ($M = 58.4\%$, $M = 0.84$) were both significant, $t(31) = 2.97$, $p < .01$ and $t(31) = 3.04$, $p = 0.005$, respectively. Effect size in these two participant samples was comparable: fMRI study $d = 0.42$; behavioral study $d = 0.56$. This suggests that the primary difference in the findings for these two experiments was the power provided by the sample sizes. In addition, it should be noted that the study and test phases in the behavioral study were conducted in the same room with very little delay between them. The fMRI study phase was completed in a small testing room and the test phase was completed inside the MRI machine. In addition, the process of preparing the participant for the MRI scan added a minimum of 30 minutes of delay between the study and test phases. These differences may partially account for the reduced behavioral effects of context reinstatement in the fMRI version of the experiment, as the environmental and temporal contexts were likely to contribute to the overall degree of context reinstatement.

We compared reaction times (RTs) to the pretrial context cue question across Match and Mismatch trials, sorted according to the eventual memory judgment on each trial. Means and standard deviations are presented in Table 1. In the fMRI experiment, there were no significant differences between response times to the pretrial study question or to the test

probe for any conditions (all $p > 0.10$.) In the behavioral experiment, there were no significant differences between response times to the pretrial study question for any conditions (all $p > 0.10$.) However, reaction times for the test probe judgment were significantly slower for Know responses than for Remember responses ($t(18) = 27.57$, $p < .001$) with no differences (all $p > 0.10$) between the Match and Mismatch conditions. This result fits with the typical pattern of RTs in a Remember/Know study in that Know responses are slower than Remember responses. This is due to the instructions which ask participants to give a Remember response if they recollect a detail and to give a Know response if they don't recollect a detail but the item seems familiar. Therefore, participants make an internal recollection judgment before assessing familiarity. The Remember vs. Know RT effect was compressed in the fMRI experiment, likely due to the shorter response window, but the results show the same numerical pattern as in the behavioral experiment.

fMRI Analyses

The first fMRI analysis assessed context reinstatement during the pretrial cue period for the predicted ordinal interaction between the factors of Match/Mismatch context and Remember/Know retrieval. The pretrial cue analyses examined only the brain activation that occurred before the test probe period, but the trials were sorted according to subsequent response type. This technique is similar to a subsequent memory analysis, which sorts encoding trials according to later retrieval performance, but novel in that we analyzed a time period during which the tested item was not being studied.

We predicted that Match Remember trials would show significant PHc activation during the pretrial cue period while all other conditions (Mismatch Remember, Match Know, and Mismatch Know) would not show pretrial cue activation associated with later retrieval status. That is, we hypothesized that pretrial cue activation would predict later recollection, but only in the Match condition. We did not predict any differences between the Mismatch Remember, Match Know, and Mismatch Know conditions. Consistent with these predictions, we found greater activation in left PHc for the Match condition, when a Remember response was ultimately given, as compared to the three remaining conditions simultaneously. This analysis produced a significant cluster in left PHc (peak voxel: x=−18, y=−34, z=−5, $t(18)=2.71$, $p=.004$, cluster=26 contiguous voxels). Figure 3A shows the activation map derived from this contrast. No suprathreshold voxels were found in either the MTL or whole-brain analyses for this interaction.

To follow-up this significant ordinal interaction, we contrasted trials in the Match Remember condition with trials in the Match Familiar condition and found a cluster of activation in left PHc (peak voxel: x=−12, y=−31, z=−5, $t(18)=3.05$, $p=.001$, cluster=24 contiguous voxels) that overlapped with the interaction analysis cluster. Figure 3C shows the activation map derived from this contrast. This result suggests that the association of left PHc with subsequent recognition is specific to recollection, a process that requires context retrieval. Table 2 lists the significant clusters found in the whole-brain analysis for this contrast.

Finally, we analyzed the contrast between Match Remember and Mismatch Remember trials during the pretrial cue period. This contrast revealed a cluster of activation in left PHc (peak voxel: x=−15, y=−37, z=−8, $t(18)=3.37$, $p=.001$, cluster=21 contiguous voxels), overlapping with the clusters found in both the interaction analysis and the Match Remember vs. Match Familiar contrast. Figure 3B shows the activation map derived from this contrast. This result

[2]This pattern was tested in a one-way, 4 condition, ANOVA with Match Remember modeled as a positive factor and the three remaining conditions modeled as negative factors (i.e., +3, −1, −1, −1 respectively.) This approach was based on proposals by Strube & Bobko (1989).

suggests that the association of left PHc with subsequent recollection is specific to the Match condition, in which the pretrial context cue was relevant to the later test probe. Table 1 lists the significant clusters found in the whole-brain analysis for this contrast.

As a further test, we verified that there were no significant differences among the three conditions with predicted low activation in the ordinal interaction. As expected, in the Mismatch condition there was no relationship between the pretrial cue period and the eventual item test probe. No suprathreshold voxels were seen in MTL, PHc, or the whole brain analysis for the Mismatch Remember vs. Know contrast. Similarly, no suprathreshold voxels were seen in MTL, PHc, or the whole brain analysis for the Match Know vs. Mismatch Know contrast. Finally, no suprathreshold voxels were seen in MTL, PHc, or the whole brain analysis for the Mismatch Remember vs. Match Know contrast.

In addition to the previous analyses of pretrial cue period activation, we assessed retrieval-related activation that followed presentation of the test probe. We compared activation for Remember responses, collapsed across the Match and Mismatch conditions, to correct rejections of new items. We found widespread activation (cluster = 444 contiguous voxels) in left MTL (see Figure 4) with peaks in both PHc (x=−21, y=−40, z=−17, $t(18)=5.81$, $p < .001$) and the hippocampus (x=−27, y=−34, z=−5, $t(18)=6.13$, $p < .001$). Whole brain analyses are presented below. We then contrasted Remember responses from the Match and Mismatch conditions to determine whether there were any differences in retrieval processing due to the pretrial cue condition. We did not find any suprathreshold voxels in MTL, PHc, or the whole brain analysis that distinguished between Match and Mismatch recollection during the test probe period. An additional follow-up analysis comparing Remember to Know responses during the test trial period did not reveal significant activation in MTL at the corrected alpha level.

Although our predictions concerned MTL activation, we also explored whole-brain activation. The contrast assessing Match Remember vs. Match Know trials during the pretrial cue period revealed activation in right anterior ventrolateral prefrontal cortex (VLPFC, see Table 2.) This region has been implicated in encoding of non-verbal information (Kirchhoff, Wagner, Maril, & Stern, 2000; Wagner et al., 1998). In fact, Machizawa and colleagues (Machizawa, Kalla, Walsh, & Otten, 2010) proposed that right VLPFC supports processing during encoding tasks (e.g. living/nonliving) that rely on judgments about nonverbal attributes of a stimulus. Activation in right VLPFC is also correlated with activation in left middle temporal cortex, which is involved in representations of perceptual object form (Dobbins & Wagner, 2005). Retrieval of visual representations of objects was likely to occur during the encoding tasks used during the pretrial cue period (e.g. “Does this item weigh less than 10 pounds?” or “Is this item fragile?”). These tasks were designed to be similar to the type of judgments made during a living/nonliving encoding task. Increased activation in right VLPFC during Match Remember trials specifically, as compared to Match Know trials, suggests that processing of visual representations during encoding increased the likelihood of later recollection, specifically during Match trials. Although we did not predict this finding, we speculate that visualization of the matching encoding context and the sham study object during the pretrial cue period increased the degree to which participants created a mental context that would then facilitate recollection of the test probe following the retrieval cue.

The contrast of Match Remember vs. Mismatch Remember during the pretrial cue period produced two areas of activation that survived the whole-brain threshold (see Table 3). The first was a cluster overlapping both the left lingual gyrus and PHc, as discussed previously.

[3]This contrast did produce MTL activation at more lenient thresholds.

A second cluster of activation was seen in bilateral ventromedial prefrontal cortex, which coactivates with and is functionally connected to PHc (Ranganath & Ritchey, 2012). Ventromedial prefrontal cortex has also been identified, along with MTL regions, as part of a large network of brain regions that contribute to recollection processes (Ranganath & Ritchey, 2012; Rugg & Vilberg, 2013). This area has been further implicated as part of a "context associations network" (Kveraga, et al., 2011) that is found when context information associated with a visual image is called to mind. Although we did not predict ventromedial prefrontal cortex activation *a priori*, the results suggest that this region may have an important role in reinstating episodic context. This exploratory finding can serve as the basis for predictions in future studies.

The same ventromedial prefrontal cortex region also surpassed our whole-brain threshold in the Match/Mismatch Remember vs. correct rejection contrast during the test probe period (see Table 4). This is consistent with the finding of recollection-associated activity during the test probe period in MTL as well. One additional finding of particular interest is the significant cluster of activation in right insula. The insula has been identified as part of a "salience" network (Sridharan, Levitin, & Menon, 2008) that, in combination with anterior cingulate cortex, is thought to be involved in exogenous direction of attention and externally cued cognitive processes. Such control processes are likely to be critical for recollection.

Discussion

The primary question addressed in this study is how context reinstatement affects episodic memory, both in cognitive processing and the neural involvement of MTL subregions. In particular, can context reinstatement act as a prime for recollection of an item cue? If so, are any MTL subregions sensitive to this reinstatement? Does activation in these regions during context reinstatement predict recollection?

Given that recollection is defined as the retrieval of context information from an item cue, context reinstatement prior to the item cue essentially reverses the temporal relationship between context and item processing during retrieval. That is, rather than an item cue exclusively driving recollection of the remaining episode (including context information), our paradigm begins with priming of the context cue. Recollection may then proceed both from activation of the relevant context information and activation of the item test probe. Context reinstatement does not affect familiarity-based retrieval because familiarity is based on strength of the item cue and does not involve contextual retrieval. Consistent with our predictions, our results indicate that PHc activation in response to cognitive context reinstatement predicts recollection, but not familiarity, up to eight seconds *before* the test item is known to the participant. This finding only holds when the reinstated cognitive context is the original, matching question presented during the item's encoding. There is no relationship between PHc activation and recollection when the reinstated cognitive context is irrelevant to the test item, such that it was not studied with the test item during encoding.

The results of from the test probe period analysis are consistent with prior evidence that successful episodic retrieval is associated with increased activation in both PHc and the hippocampus. This pattern of activation is predicted by several theories of MTL subregion function (e.g. Aggleton & Brown, 2006; Brown & Aggleton, 2001; Davachi, 2006; Eichenbaum, Otto, & Cohen, 1994), including the BIC theory (Diana et al., 2007; Eichenbaum et al., 2007). We did not find differences in activation in PHc or the hippocampus when comparing the Match condition to the Mismatch condition during the test probe period. Although the Match condition led to greater PHc activation during the pretrial period, this finding does not appear to be due to lower power or weaker memory overall in the Mismatch condition. The Mismatch condition shows an equally large (and

quite strong) significant activation during the test probe period to that seen in the Match condition. This finding of similar activations during retrieval serves as a clear contrast to the one-sided activation (Match but not Mismatch) during the pre-trial period.

The BIC theory predicts different types of information processing in the subregions of MTL. We found some evidence for a unique pattern of activation in PHc as compared to the hippocampus and PRc. PRc activation was not significantly associated with recollection either during the pretrial cue period or the test probe period. Hippocampal activation was associated with successful recognition following the test probe but not associated with context reinstatement during the pretrial cue period. Thus PHc may be important for context processing while the hippocampus is important for linking such context to an event but not for processing context information in the absence of an episodic link. This evidence for a distinct role for PHc in context processing converges with the conclusions from our prior adaptation study (Diana et al., 2012). In that study we found adaptation in PHc to repeated encoding of a context (the same study questions used in the current experiment), whereas activation in the hippocampus and PRc were not modulated by repeated encoding of the context. Thus the current study indicates PHc processing during *retrieval* of a context, whereas the prior study (Diana et al., 2012) indicates PHc processing during *encoding* of a context.

The finding that PHc activation during the pretrial cue period predicts later recollection is unlikely to be driven by either effortful or spontaneous retrieval prior to the item test probe. Effortful retrieval is unlikely because participants were engaged in studying a new item with the encoding question and were told that this was their task during the pretrial cue period. The majority of our participants (17 out of 19) reported that they were unaware of any relationship between the pretrial cue and its following test item, meaning that they did not view the two portions of the trial as associated. Spontaneous retrieval is unlikely because we designed the experiment so that each question was used as the encoding task for eight individual words during the initial study phase. Each question was also presented with additional study words throughout the test list. If participants spontaneously recalled an item during context reinstatement, the probability that any given recalled item would be the test probe was at most 1 in 8 (decreasing in likelihood as the questions were repeated during the test list).

Previous studies have found that a familiar context, such as our reinstated encoding questions, may spuriously increase the likelihood of a familiarity-based response to an item (e.g. Diana, Peterson, & Reder, 2004; Graf & Ryan, 1990). However, this effect does not rely on linking the item to the correct context. This means that the effect would occur for both recollected and familiar items. In fact, if such an influence on pretrial cue period activation occurred it would not affect our conclusions. Spurious familiarity-based item responses due to a familiar context would increase the degree to which PHc activation during the pretrial cue period predicts Know responses, the opposite of our finding. Thus, any effect of context familiarity in the absence of episodic recollection would indicate that our results underestimate the size of the context reinstatement effect.

The influence of cognitive context reinstatement on recollection is evidence for the usefulness of transfer appropriate processing (Morris, Bransford, & Franks, 1977). Transfer appropriate processing proposes that similarity between encoding and test contexts facilitates retrieval of a studied item. In effect, context reinstatement moves the test event closer to the original study context. This principle is also plausible from a neural standpoint. Memory retrieval can be conceptualized as using a cue, physically instantiated in a pattern of neural firing, to retrieve a complete event, which is a connected or overlapping neural pattern (see Carr, Rissman, & Wagner, 2010; Nakashiba et al., 2012 for studies on pattern

completion). Therefore, recreating the state in which that cue was originally processed should activate a second neural pattern (in addition to the cue) that connects to or overlaps with the pattern for the complete event.

At least one prior study has demonstrated that similarity between encoding and context reinstatement indicates successful recollection of a prospective memory task (Gilbert, Armbruster, & Panagiotidi, 2012). However, this voxelwise pattern of similarity was not localized to a particular brain region. The current study suggests that a key region within the overall voxelwise pattern of activation across the brain may be parahippocampal cortex. In addition, the current experiment provides evidence relevant to a question raised by that study's conclusions: brain activation during context reinstatement can predict later retrieval and is not limited to serving as a marker of successful retrieval.

Cognitive context may be related to Kahana and colleagues' (Howard, Kahana, & Wingfield, 2006; Polyn & Kahana, 2008; Sederberg, Howard, & Kahana, 2008) definition of temporal context as the "mental cache" of recent experience, but the two concepts are not equivalent. Many studies have demonstrated a role for the medial temporal lobes (MTL) in the processing of temporal context (Jenkins & Ranganath, 2010; Kumaran & Maguire, 2006; Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Tubridy & Davachi, 2011; Turk-Browne, Scholl, Johnson, & Chun, 2010). These studies of temporal context tend to define context based on the sequence of preceding and following items in a list. Thus temporal context is typically measured according to the relative position of items on a study list. Cognitive context, as we define it, differs from temporal context in that cognitive context includes only those recent experiences that reach conscious awareness during the study event. Cognitive context also includes new associations that arise during encoding, such as elaborating upon the study item, and may or may not be associated with surrounding events.

Several questions present themselves based on the results of this experiment. Although BIC theory does not limit the definition of context or PHc function to spatial information alone, the current data do not speak to this issue. We used verbal encoding questions that did not require mental imagery or spatial processing, but some of the questions lend themselves to mental imagery or the visualization of scenes. In those cases where visual imagery was used, recollection is likely to be at least partially driven by retrieval of spatial information. Further experiments could examine context reinstatement when the contexts are nonspatial or even nonvisual in order to assess whether these findings rely on spatial information.

Although previous studies have found that PRc activation is associated with familiarity-based responses, we did not find a relationship between PRc and Know judgments. There was no significant activation in PRc during either the pretrial cue period or the test probe period. Given the likelihood of reduced signal-to-noise ratio in PRc due to artifacts, we do not wish to make conclusions based on the lack of an effect in PRc.

Finally, the present study may underestimate the relationship between context reinstatement and PHc activation. Our manipulation did not reinstate the identical item-context binding experienced during the study phase. Although we repeated the encoding question at test, novel words were processed with the encoding question during reinstatement. For example, the question "Could this item melt?" might be studied with the word "VIOLIN" at encoding. If "VIOLIN" was tested in the Match condition, context reinstatement would consist of the word "CLOSET" studied with the same question. Although these two states of mind have a similar gist, the semantic associations that emerge for each word may be quite different. Ideally future studies would recreate the context as precisely as possible so as not to underestimate the effects of context reinstatement in the brain.

The previous point brings up an additional idea for consideration. If one accepts that context is a type of information that is processed in episodic memory, we do not know whether that context is processed or represented as a single, unified whole (e.g. “The grocery store”) or as a series of associated details (e.g. shopping cart, produce, cash registers, Muzak®). If context is processed as a series of associated details, reinstating a portion of the context should be an effective cue to a specific event, even when other contextual information is changed. If context is processed as single, unified representation containing multiple details, reinstating only a single contextual detail should be a relatively ineffective means of reactivating an event. Therefore, our results lean toward the “associated but independent details” account rather than the “single, unified whole” account. This conclusion is preliminary at best and further research is needed. An additional prediction of these two possibilities is that overlap between previously experienced contexts is either common, according to the “associated but independent details” account, or relatively rare, according to the “single, unified whole” account.

Conclusions

Our findings support the claim that PHc plays a role in the encoding and retrieval of context information in episodic memory (see also Diana, Yonelinas, & Ranganath, 2012). This is true even when item information is not yet activated and the item-context binding has not been retrieved. In addition, PHc is responsive to reinstatement of the cognitive processing that occurred during an event. Finally, these results suggest that item and context information can play similar roles in triggering recollection of an episodic memory.

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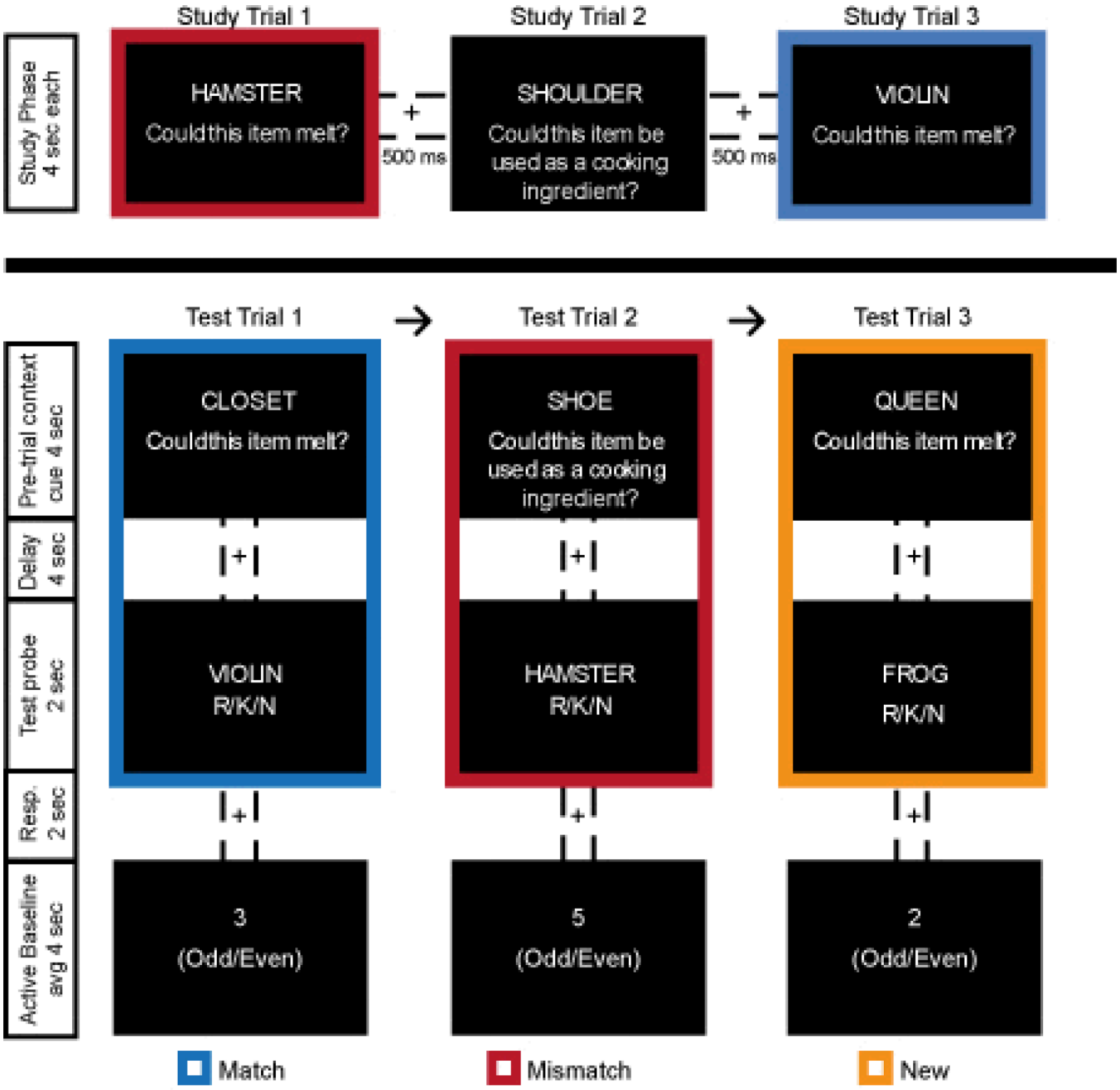

Figure 1.
Schematic of trial design and timing at study and test. Each test trial had three parts: pre-trial context cue, delay, and test probe. An active baseline task (odd/even judgments) was used between test trials. Outline color indicates study trials that will later be tested in either the Match or Mismatch condition and test trials that have a Matched or Mismatched pretrial-context cue.

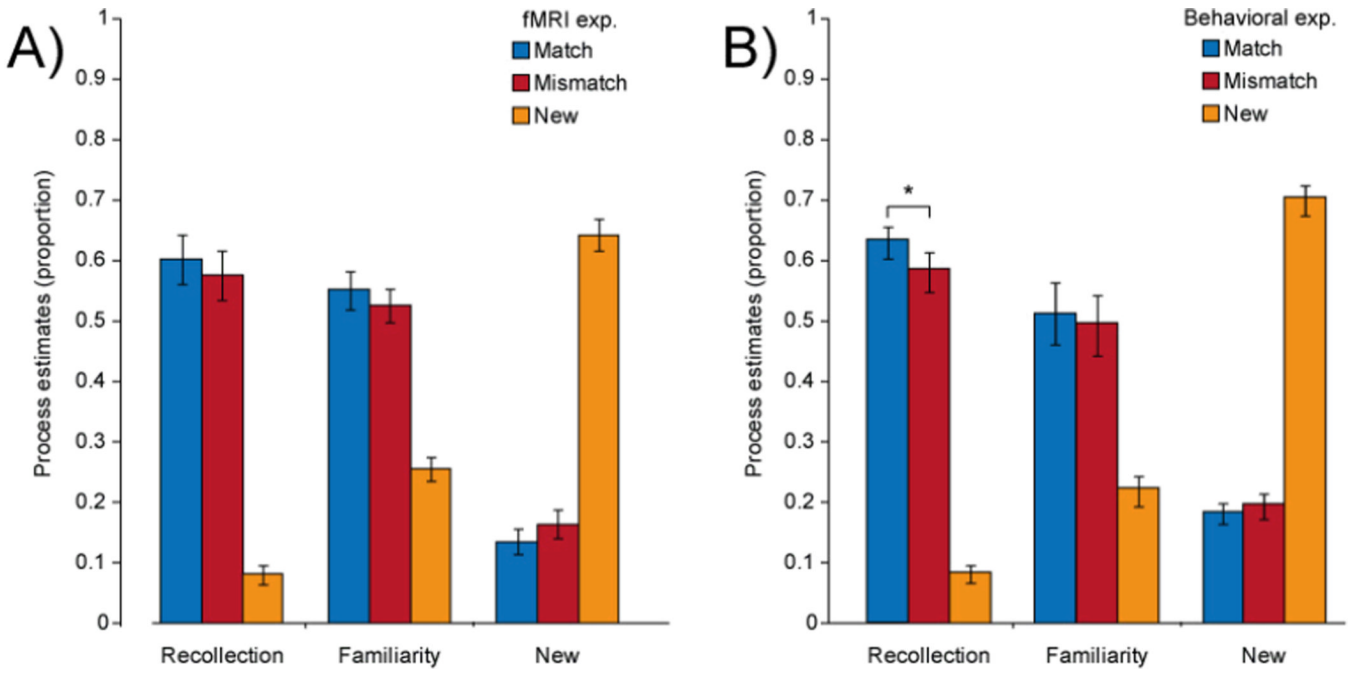

Figure 2.

Recollection, the proportion of Remember responses, and familiarity, measured as F = Know(1 – Remember), process estimates (see Yonelinas & Jacoby, 1995) for the Match, Mismatch, and New conditions in both the fMRI experiment (panel A) and a separate behavioral experiment (panel B) using the same stimuli and procedure but different participants. Error bars indicate the standard error of the mean. *$p < .05$

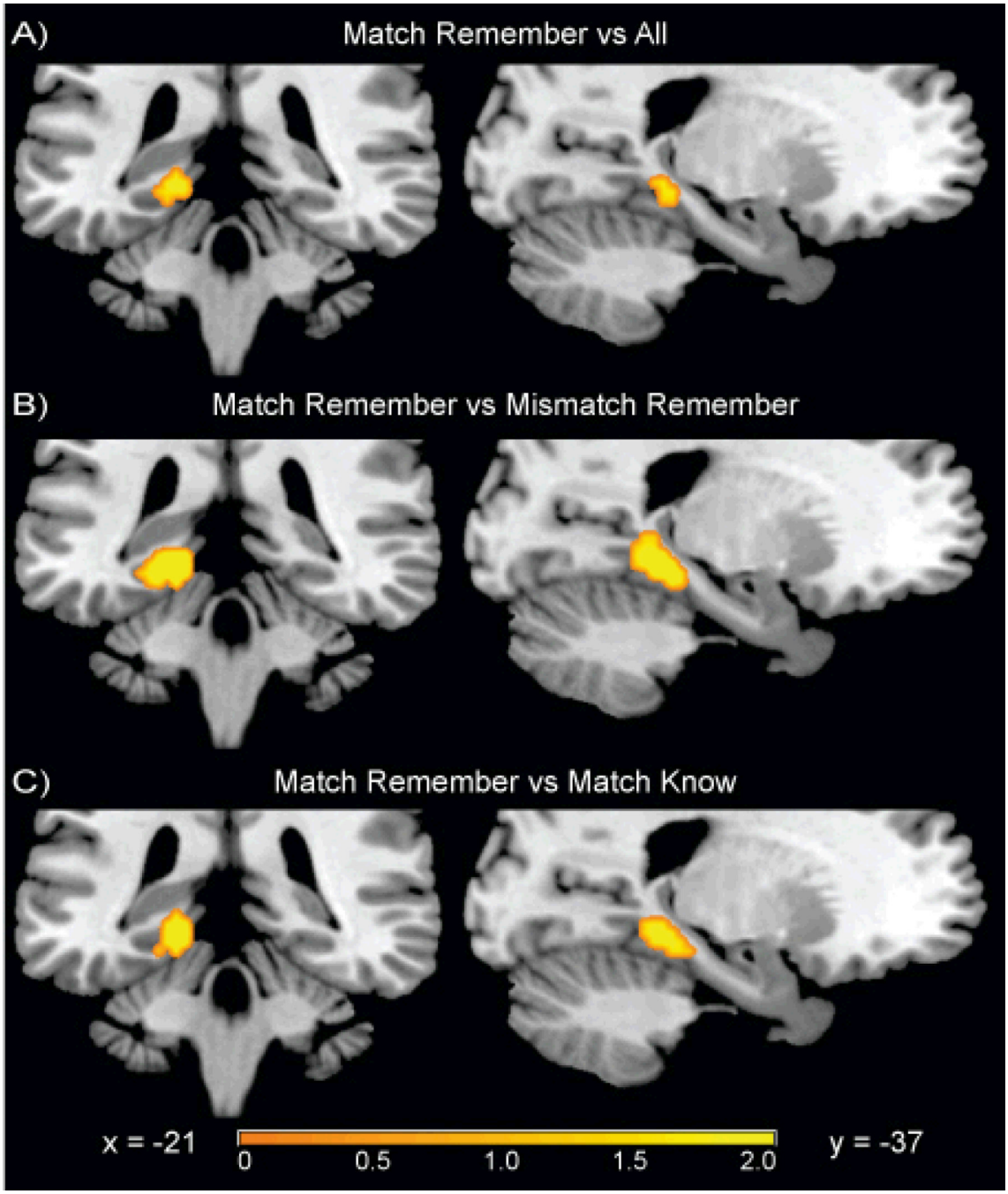

Figure 3.
Pretrial cue period PHc activation maps for the contrasts of: A) Match Remember vs. All (Mismatch Remember, MatchKnow, and MismatchKnow.) No additional clusters in either the MTL or whole brain analyses surpassed the cluster-corrected alpha-level. B) Match Remember vs. Mismatch Remember. Whole-brain findings for this contrast are presented in Table 2. No additional clusters in the MTL analysis surpassed the cluster-corrected alpha-level. C) Match Remember vs. Match Know. Whole-brain findings for this contrast are presented in Table 3. Images are presented in neurological convention such that the left hemisphere corresponds to the left side of the image.

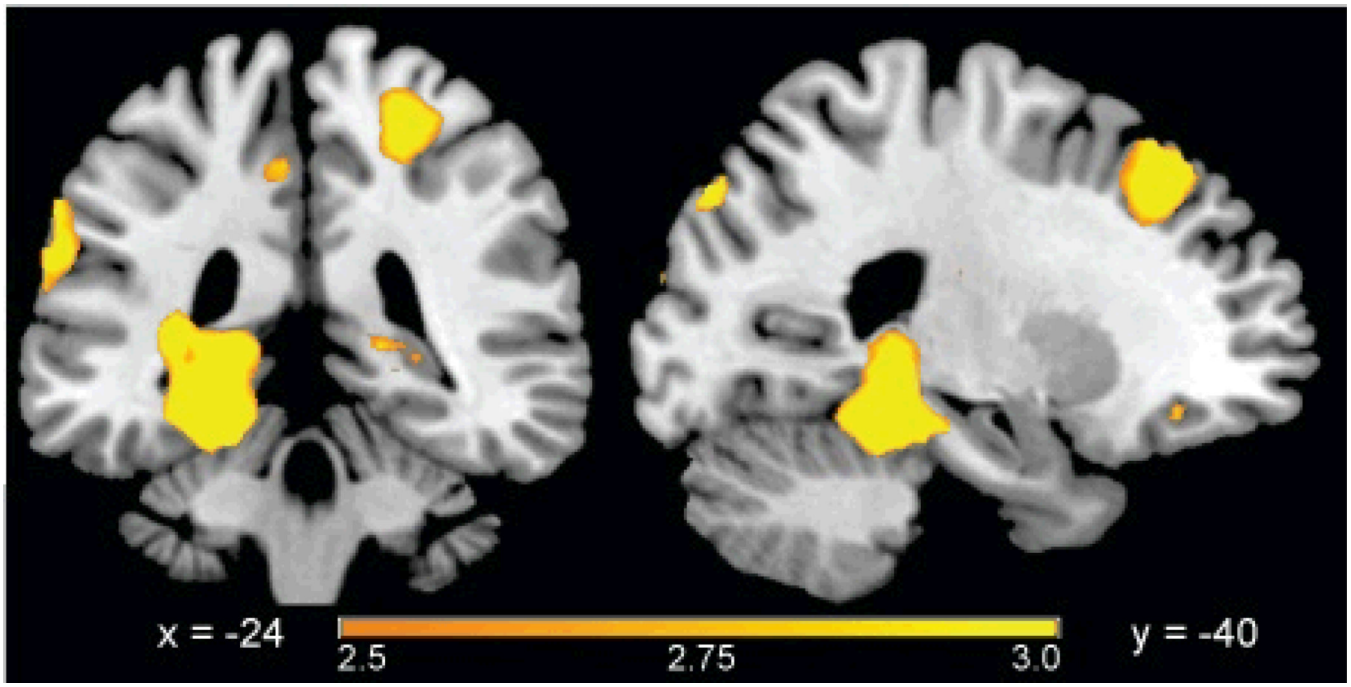

Figure 4.

A) Test probe period activation map for overall (Match and Mismatch combined) correct Remember vs. overall correct New judgments. See Table 4 for coordinates, cluster sizes, and region labels. No differences were found between Match and Mismatch trials in the analysis of the test probe period.

Table 1

Reaction times in response to the pretrial cue question (yes/no) and the test probe (Remember/Know/New) in both the fMRI experiment and the behavioral experiment. Standard deviations are listed in parentheses.

Reaction Times (ms)		Pretrial Cue Judgments		Test Probe Judgments	
		Remember	Know	Remember	Know
fMRI	Match	2023 (397)	2118 (339)	1246 (265)	1288 (242)
	Mismatch	2111 (361)	2105 (287)	1334 (170)	1354 (173)
Behavioral	Match	1479 (219)	1444 (265)	1497 (434)	1828 (391)
	Mismatch	1445 (201)	1441 (209)	1434 (320)	1827 (329)

Table 2

Peak voxels at $p_{corrected}<.05$ for whole-brain analyses of the pretrial cue period Match Remember vs. Mismatch Remember analysis. (Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.)

Brain Region	x	y	z	t	cluster
Right Ventromedial Prefrontal Cortex	6	20	−11	4.72	123
Left Ventromedial Prefrontal Cortex	−9	20	−11	3.75	-
..	−15	32	−14	3.55	-
Left Lingual Gyrus	−9	−25	−8	3.38	80
Left Parahippocampal Cortex	−15	−37	−8	3.37	-

Table 3

Peak voxels at $p_{corrected}<.05$ for whole-brain analyses of the pretrial cue period Match Remember vs. Match Know analysis. (Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.)

Brain Region	x	y	z	t	cluster
Right Anterior Ventrolateral Prefrontal Cortex	44	48	−8	3.88	202
..	36	56	1	3.47	-
..	35	44	12	3.55	-

Table 4

Peak voxels at $p_{corrected}<.05$ for whole-brain analyses of the test probe period Match/Mismatch Remember vs. Correct Rejection analysis. (Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.)

Brain Region	x	y	z	t	cluster
Left Middle Temporal Gyrus	−48	−76	25	9.56	758
Left Precuneus	−12	−85	40	6.1	-
Left Inferior Temporal Lobe	−57	−58	−5	6.4	-
Left Hippocampus	−27	−34	−5	6.13	444
Left Parahippocampal Cortex	−21	−40	−17	5.81	-
Left Lingual Gyrus	−18	−40	4	5.43	-
Left Ventromedial Prefrontal Cortex	−12	38	−11	4.35	178
..	−9	26	−11	3.47	-
Left Middle Frontal Gyrus	−27	32	52	4.21	84
..	−24	29	43	4.01	-
Right Insula	33	−16	4	4.1	139
..	39	−13	19	3.84	-
Right Caudate	33	−31	7	3.84	-

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