

Published in final edited form as:

J Cogn Neurosci. 2011 December ; 23(12): 3959–3971. doi:10.1162/jocn_a_00086.

Neural Correlates of Confidence during Item Recognition and Source Memory Retrieval: Evidence for Both Dual-process and Strength Memory Theories

Scott M. Hayes^{1,2,3}, Norbou Buchler⁴, Jared Stokes⁵, James Kragel⁵, and Roberto Cabeza^{5,6,7}

¹Memory Disorders Research Center, VA Boston Healthcare System & Boston University School of Medicine

²Neuroimaging Research Center, VA Boston Healthcare System

³Department of Psychiatry, Boston University School of Medicine

⁴U.S. Army Research Lab, Aberdeen Proving Ground

⁵Center for Cognitive Neuroscience, Duke University

⁶Brain Imaging and Analysis Center, Duke University Medical Center

⁷Center for the Study of Aging and Human Development, Duke University Medical Center

Abstract

Although the medial-temporal lobes (MTL), PFC, and parietal cortex are considered primary nodes in the episodic memory network, there is much debate regarding the contributions of MTL, PFC, and parietal subregions to recollection versus familiarity (dual-process theory) and the feasibility of accounts on the basis of a single memory strength process (strength theory). To investigate these issues, the current fMRI study measured activity during retrieval of memories that differed quantitatively in terms of strength (high vs. low-confidence trials) and qualitatively in terms of recollection versus familiarity (source vs. item memory tasks). Support for each theory varied depending on which node of the episodic memory network was considered. Results from MTL best fit a dual-process account, as a dissociation was found between a right hippocampal region showing high-confidence activity during the source memory task and bilateral rhinal regions showing high-confidence activity during the item memory task. Within PFC, several left-lateralized regions showed greater activity for source than item memory, consistent with recollective orienting, whereas a right-lateralized ventrolateral area showed low-confidence activity in both tasks, consistent with monitoring processes. Parietal findings were generally consistent with strength theory, with dorsal areas showing low-confidence activity and ventral areas showing high-confidence activity in both tasks. This dissociation fits with an attentional account of parietal functions during episodic retrieval. The results suggest that both dual-process and strength theories are partly correct, highlighting the need for an integrated model that links to more general cognitive theories to account for observed neural activity during episodic memory retrieval.

INTRODUCTION

Decades of memory research have shown that the act of remembering can result in a wide range of phenomenological experiences. On one end, memory retrieval can result in a vague notion of having seen something before, and at the other end, remembering can result in a rich and vivid “reliving” of a previous experience. At a theoretical level, a critical question is what process or processes underlie these two experiences. According to dual-process theories (Buchler, Light, & Reder, 2008; Yonelinas, 2002; Jacoby, 1991; Mandler, 1980), episodic retrieval depends on two independent processes: *familiarity*, which refers to processing a continuous memory strength signal, and *recollection*, which refers to the recovery of source memory information, such as context surrounding the original event. An influential theory, the dual-process signal detection model, assumes that familiarity is a graded process (quantitative) whereas recollection is threshold process (qualitative; Yonelinas, Aly, Wang, & Koen, 2010; Yonelinas, 1994). When recollection fails, retrieval decisions are based on familiarity. In contrast, according to *strength theories*, episodic retrieval reflects a *single memory strength* dimension. A recent strength theory, the aggregate-strength model, incorporates the familiarity–recollection distinction by assuming that both processes are graded and are aggregated into a single strength signal before the retrieval decision (Wixted, Mickes, & Squire, 2010; Mickes, Wais, & Wixted, 2009; Wixted, 2007).

Dual-process and strength theories also differ regarding the contributions of specific brain regions to episodic retrieval. For the most part, the debate has centered on regions of the medial-temporal lobes (MTL). Dual-process theories have proposed that familiarity is more dependent on rhinal cortex whereas recollection is more dependent on the hippocampus (Eichenbaum, Yonelinas, & Ranganath, 2007; Aggleton & Brown, 1999). Evidence consistent with this hypothesis has been reported in many fMRI studies (for reviews, see Diana, Yonelinas, & Ranganath, 2007; Skinner & Fernandes, 2007). In general, these studies distinguished recollection and familiarity by comparing item recognition decisions (old or new?), which are assumed to involve an important familiarity component, to source memory decisions (e.g., where? when? or how?), which are assumed to be critically dependent on recollection. In contrast with dual-process theories, strength theories posit the involvement of both the hippocampus and rhinal cortex in both recollection and familiarity (Squire, Wixted, & Clark, 2007). Strength theories argue that the hippocampal–rhinal dissociations found in fMRI studies reflect a confound of memory strength: Successful source memory requires strong memories, whereas successful item recognition may reflect weak memories. Thus, an alternative interpretation of fMRI findings proposes that the hippocampus is more sensitive to strong memories (reflecting both familiarity and recollection) whereas rhinal cortex is more sensitive to weak memories (reflecting both familiarity and recollection; Wais, 2008, 2011; Wais, Squire, & Wixted, 2010; Squire et al., 2007).

In the current study, we investigated dual-process and strength accounts of hippocampal and rhinal contributions to episodic retrieval using a factorial approach. The design crossed a quantitative manipulation of memory strength (high vs. low confidence) with a qualitative manipulation of recollection versus familiarity (source vs. item memory tasks). Strength theory (aggregate-strength version; Wais, 2008; Squire et al., 2007) assumes that confidence ratings reflect memory strength both in the item and source memory tasks; hence, it predicts that in both tasks the hippocampus should be activated by high-confidence trials (strong memories) and rhinal cortex, by low-confidence trials (weak memories). In contrast, dual-process theory (Diana et al., 2007; Eichenbaum et al., 2007) assumes that confidence ratings reflect qualitatively different processes in item recognition versus source memory tasks; hence, it predicts dissociations between these tasks. That is, in item recognition tasks, high-

confidence responses may reflect familiarity as well as recollection, whereas in source memory tasks, high-confidence responses reflect primarily recollection. Low-confidence source memory responses may reflect guessing. Thus, dual-process theory predicts that the rhinal cortex should show confidence effects in the item but not in the source memory task, whereas the hippocampus should show greater confidence effects in the source memory task (because high-confidence source retrieval relies on recollection to a greater extent than item retrieval, which can be mediated by familiarity and recollection). In summary, whereas strength theory predicts a main effect of confidence, dual-process theory predicts a confidence by task interaction.

In addition to the MTL, the current study also investigated two other core components of the episodic memory retrieval network (Cabeza & Nyberg, 2000): the lateral PFC and the posterior parietal cortex. Evidence that PFC is important for episodic memory retrieval comes from patients (e.g., Johnson, O'Connor, & Cantor, 1997; Shimamura, Janowsky, & Squire, 1990; Janowsky, Shimamura, & Squire, 1989) as well as neuroimaging studies (Hayes, Ryan, Schnyer, & Nadel, 2004; Cabeza, Locantore, & Anderson, 2003; for a review, see Mitchell & Johnson, 2009; Yonelinas, 2002). PFC activation patterns tend to differ across hemispheres. The left PFC regions tend to show greater activity for source than item memory consistent with a role in recollection (Skinner & Fernandes, 2007). However, in some studies, the left PFC activity during source memory tasks is not sensitive to retrieval success (Kahn, Davachi, & Wagner, 2004; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins, Foley, Schacter, & Wagner, 2002), suggesting it reflects an orientation toward recollection ("recollective orienting") rather than recollection per se. The right PFC regions have been found to show greater activity for low- than high-confidence retrieval suggesting familiarity or the processing of weak memory signals (Fleck, Daselaar, Dobbins, & Cabeza, 2006; Henson, Rugg, Shallice, & Dolan, 2000). More recently, PFC has received increasing attention in the single- versus dual-process debate. For instance, it has recently been reported that hippocampal and perirhinal regions track subsequent memory strength, whereas PFC regions track subsequent recollection (Kirwan, Wixted, & Squire, 2008). Recent work in patients with frontal lobe damage have further highlighted the role of PFC in recollection and source memory (Duarte, Ranganath, & Knight, 2005; Simons et al., 2002; Yonelinas, 2002).

Beyond the MTLs and PFC, recent functional neuroimaging reviews have emphasized parietal cortex as a significant contributor to episodic memory retrieval (Olson & Berryhill, 2009; Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In contrast to PFC, parietal activation patterns tend to differ along a ventral–dorsal dimension rather than across hemispheres. Ventral parietal cortex (VPC; BA 39–BA 40) has been associated with recollection and high-confidence retrieval conditions, whereas dorsal parietal cortex (DPC; lateral and medial BA 7) has been associated with familiarity and low-confidence retrieval conditions (Cabeza et al., 2008; Vilberg & Rugg, 2008). Data demonstrating increased activity for "remember" versus "know" responses in parietal cortex have been interpreted as additional support for dual-process accounts of recognition memory (e.g., Vilberg & Rugg, 2009). The prevalence of functional neuroimaging studies implicating parietal regions in episodic memory has resulted in increased scrutiny of episodic memory function in patients with parietal lobe damage. The handful of studies reported to date suggest that parietal lobe damage may not reduce memory accuracy (Ally, Simons, McKeever, Peers, & Budson, 2008; Simons et al., 2008) but may result in reductions in subjective recollective experiences (Ally et al., 2008; Davidson et al., 2008; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007) or confidence (Simons, Peers, Mazuz, Berryhill, & Olson, 2010).

Although the dual-process and strength accounts originally focused on behavioral data, neuroimaging data are used as evidence for strength or dual-process theories. For instance, previous studies focusing on encoding related activity in the MTLs have found evidence for dual-process (Ranganath et al., 2004; Davachi, Mitchell, & Wagner, 2003) or strength (Kirwan et al., 2008; Shrager, Kirwan, & Squire, 2008) accounts. In the current study, we examine support for strength or dual-process accounts during episodic memory retrieval within the MTLs as well as explore whether strength or dual-process theories may account for patterns of activity in PFC and parietal regions. Given the aforementioned confound between recollection–familiarity and memory strength, PFC and parietal activation patterns can be accommodated by both dual-process and strength theories: The left PFC and VPC can be attributed either to recollection or to the processing of strong memories, whereas the right PFC and DPC can be attributed either to familiarity or to the processing of weak memories. As in the case of the MTL, the factorial design of the current study can help distinguish these alternative interpretations because strength theory predicts a main effect of confidence, whereas dual-process theory predicts dissociations between item and source memory tasks.

METHODS

Participants

Nineteen healthy young adults recruited from the Duke community were screened for contraindications to MRI and participated in the study. Three participants were excluded because they had fewer than 10 trials in one of the conditions, resulting in a final sample size of 16 participants (mean age = 21.6 years, $SD = 2.3$ years; mean education = 14.4 years, $SD = 1.7$ years; seven women). All participants gave written informed consent and received financial compensation. All experimental procedures were approved by the Duke University Institutional Review Board.

Behavioral Methods

Materials—Stimuli consisted of 440 English words collected from the Medical Research Council psycholinguistic database (Coltheart, 1981) with normative word frequencies in the lexicon of 5–15 per million, $M = 8.8$ (3.1; Kucera & Francis, 1967) and mean length of $M = 7.1$ (2.3) letters. Unique study and test lists were randomly generated for each participant and words were assigned to the following conditions: item (180), source (180), or item lures (80 words—presented only at retrieval). There were four encoding lists, each composed of 130 trials. Within each list, 50 words presented once and 40 words presented twice. Repetition was manipulated to encourage variability in response confidence. At retrieval, there were four item test lists, each consisting of 45 targets (studied words) and 20 lures (nonstudied words), and four source test lists, each consisting of 45 studied words.

Encoding—Participants studied words under intentional encoding conditions while outside the scanner. Words were presented on a 19-in. computer monitor in black font on a gray background for 3 sec with a 1-sec intertrial interval using a PC with Cogent, a stimulus presentation toolbox within MatLab 6.5.1. Participants made a “pleasant/unpleasant” judgment for half of the trials and a “bigger/smaller than a shoebox” judgment for the other half. These judgments were evenly divided between single- and twice-presented trials. Subjects were presented with the same judgment task when an item was repeated. Subjects completed a short study–test practice session (10 items) to confirm comprehension of the encoding task as well as item and source retrieval tasks.

fMRI Methods

Retrieval—Participants were placed supine on the MRI (General Electric 3.0 T Signa Excite HD short bore scanner [Milwaukee, WI], equipped with an eight-channel head coil) table, fitted with earplugs and earphones (and MRI-compatible corrective lenses if needed), and had their heads stabilized with cushions. The participants were moved into the bore of the scanner, and a three-plane localizer scan was collected to align whole-brain functional images that were acquired parallel to the AC–PC plane using a spiral-in gradient-echo sequence (Truong & Song, 2008; Pruessmann, Weiger, Bornert, & Boesiger, 2001): slice order = interleaved, matrix = 64^2 , field of view = 24 cm, repetition time = 2000 msec, echo time = 27 msec, sections = 34, thickness = 3.8 mm, interscan spacing = 0, flip angle = 60, SENSE reduction factor = 2. During item retrieval scans, participants made old/new responses on a 4-point confidence scale: *definitely old*, *probably old*, *probably new*, *definitely new*. During source retrieval scans, participants made source judgments on a 4-point scale: definitely pleasant/unpleasant, probably pleasant/unpleasant, probably bigger/smaller, definitely bigger/smaller. There were four item and four source functional runs, presented in consecutive blocks to minimize the effects of task switching. Source retrieval runs (study–test delay: approximately 28 min) occurred before item runs (study–test delay: approximately 45 min) to equate for retrieval difficulty. All retrieval stimuli were presented for 3 sec, with a white crosshair presented for fixation during the intertrial interval. Stimulus order and intertrial jitter (range = 1–7 sec) were determined by a genetic algorithm designed to maximize statistical efficiency and facilitate deconvolution of the hemodynamic response (Wager & Nichols, 2003). Retrieval stimuli were presented via a mirror in the scanner head coil and a rear projection system using a PC computer with Cogent. Button responses were recorded using a magnetically shielded four-button box held in the participant's right hand. Following functional imaging, a high-resolution spoiled gradient echo (SPGR) series (1-mm sections covering whole-brain, interscan spacing = 0, matrix = 256^2 , flip angle = 30, repetition time = 22 msec, echo time = 3 msec, field of view = 19.2 cm) was collected. After completion of scanning, participants were debriefed. Total scan time, including breaks and structural scans, was approximately 1 hr 40 min (Figure 1).

Image Processing and Analysis

Functional data were processed using SPM5 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, www.fil.ion.ucl.ac.uk/spm). The first four images were discarded to allow for scanner equilibrium. Images were corrected for asynchronous slice acquisition (slice timing: reference slice = 17, acquisition time [TA] = 1.97) and realigned to the first functional image within series to correct for head motion. Functional images were coregistered to the high-resolution anatomical scan, normalized to standard space (Montreal Neurological Institute [MNI] space; SPM5 defaults; original 3.8 mm³ voxel size maintained), and smoothed (8 mm isotropic kernel). The hemodynamic response for each trial was modeled using the canonical hemodynamic response function. Serial correlations were estimated using an autoregressive AR (1) model. Data were high-pass filtered using a cutoff of 128 sec, and global effects were removed (session specific grand mean scaling).

Analyses were completed using a 2 (Task: source vs. item) \times 2 (Confidence: high vs. low) ANOVA of hits in SPM 5. Whole-brain analyses, with a specific interest in PFC and parietal cortex, were completed using a cluster extent threshold of $p < .05$ corrected for multiple comparisons as indicated by Monte Carlo simulations (Slotnick, 2010). This procedure relies on the notion that the probability of observing clusters of activities because of noise decreases with increasing cluster size. The simulation consisted of 10,000 independent iterations where brain volume was modeled using a $64 \times 64 \times 34$ matrix and assuming a Type 1 error voxel activation probability of .01. The simulations resulted in a cluster extent threshold of 15 original voxels (824 mm³), and a threshold of 20 voxels (1098 mm³) was

implemented as additional protection against Type 1 error. For the a priori MTL ROI analyses, an MTL mask was created with the automated anatomical labeling atlas (Tzourio-Mazoyer et al., 2002) included in Wake Forest University PickAtlas (Maldjian, Laurienti, & Burdette, 2004; Maldjian, Laurienti, Kraft, & Burdette, 2003) and consisted of bilateral hippocampus, parahippocampal gyrus, amygdala, and fusiform gyrus. Significant Task (source vs. item) \times Confidence (high vs. low) interactions were identified, $p < .05$, extent threshold = 5 voxels (e.g., [high > low confidence correct source] > [high > low confidence correct item]). Results were then inclusively masked with main effects of within condition confidence, $p < .05$, extent threshold = 5 voxels, (e.g., high > low confidence correct source) to confirm the direction of the interaction effect. The conjoint probability following inclusive masking approaches $p = .0025$, and associated t values in Table 2 reflect the minimum t statistic. All reported coordinates are in MNI space. Brain figures were created using MRIcron (www.mricro.com; Rorden & Brett, 2000).

RESULTS

Behavioral Results

Accuracy—Table 1 shows the hit rates, false alarm rates, and corrected recognition scores (hits – false alarms) by response confidence and task. In the current design, a source miss is akin to a false alarm (incorrectly responding that the word was encoded in Condition A (false alarm) when it was actually encoded under Condition B (hit)). Therefore, we used the proportion of source misses as a measure of source false alarms and used these values to generate source corrected recognition scores. Results of a 2 (Confidence: high vs. low) \times 2 (Memory task: item vs. source) repeated measures ANOVA of corrected recognition scores revealed a significant main effect of Confidence (high > low), $F(1, 15) = 53.48$, and no effect of Task, $F < 1$. The Task \times Confidence interaction was significant, $F(1, 15) = 55.04$, $p < .001$, reflecting a greater confidence effect in the item than in the source memory task. A similar interaction was found in an ANOVA including only hits, $F(1, 15) = 32.35$, which are the trials included in fMRI analyses. Thus, greater confidence effects on item than source memory activity should be interpreted with caution because they could reflect a stronger behavioral effect that is partially driven by a floor effect for low-confidence item trials. Conversely, greater confidence effects on source than item memory activity could not be explained by behavioral differences.

fMRI Results

Medial Temporal Lobes—To test strength theory, we compared high-confidence (strong memory) > low-confidence (weak memory) trials collapsed across item and source memory tasks. Consistent with this theory, we found a significant activation in the right hippocampus (see Figure 2A). The reverse contrast (weak > strong collapsed across tasks) resulted in activation restricted to the parahippocampal gyrus, including right rhinal cortex and posterior parahippocampal cortex (see Table 2), which is also consistent with a strength account. To test the dual-process theory, we examined Confidence \times Task interaction analyses. Consistent with dual-process theory, these analyses yielded a double dissociation between the hippocampus and rhinal cortex: A right hippocampal region (extending into parahippocampal cortex) showed confidence effects (high > low) in the source but not in the item memory task (see Figure 2B), whereas bilateral rhinal regions showed confidence effects (high > low) in the item but not in the source memory task (see Figure 2C). Thus, MTL findings supported both strength and dual-process theories.

Prefrontal Cortex—To test strength theory, we investigated main effects of confidence. The strongest activations were found for the low > high confidence contrast, which yielded a large activation in right ventrolateral PFC (see Figure 3A). This region was involved in

processing weak memories for both item and source memory tasks. A familiarity interpretation of this activation is less convincing because dual-process models assume that correct source memory decisions are driven mainly by recollection. To test dual-process theory, we investigated qualitative differences between tasks as well as Task \times Confidence interactions. As illustrated by Figure 3B, several left PFC regions, including ventrolateral, anterior, and dorsal areas, showed greater activity for source than item memory tasks. Although consistent with a dual-process account, the fact that these regions did not show a confidence effect in the source task suggests that they may reflect an orientation toward recollection rather than recollection per se.

Parietal Cortex—Consistent with strength theory, we found that parietal activations tracked quantitative differences in confidence rather than qualitative differences in task: VPC showed greater activity for high than low confidence in both tasks (see Figure 3C), whereas DPC showed greater activity for low than high confidence in both tasks (see Figure 3D). Dual-process theory predicted that VPC would be sensitive to confidence (high > low) in the source memory task, reflecting recollection, whereas DPC would be sensitive to confidence in the item memory task, reflecting familiarity. The current parietal findings do not appear to fit well with a dual-process account. Indeed, a VPC region showed a Confidence \times Task interaction because confidence effects were greater in the item than the source task (see Table 2), which is inconsistent with a dual-process theory, given that VPC is thought to reflect recollection.

DISCUSSION

We found support for both dual-process and strength theories, although support for one account versus another varied depending on which of the primary nodes of the episodic memory network were considered. Within MTL, we found a right hippocampal region that responded to confidence in the item and source memory tasks (Figure 2A), supporting the strength theory. However, we also found a hippocampus–rhinal dissociation supporting dual-process theory: Whereas a right hippocampal region (near the hippocampal region showing memory strength effects) showed a confidence effect only in the source memory task consistent with recollection (Figure 2B), bilateral rhinal cortex showed a confidence effect only in the item memory task consistent with familiarity (see Figure 2C). Within PFC, several left hemisphere regions showed greater activity for source than item memory, regardless of confidence (Figure 3B), suggesting an orientation to recollection, whereas a ventrolateral right hemisphere region showed greater activity for low than high confidence in both tasks, consistent with strength theory. Finally, parietal findings were consistent with strength theory, as both tasks showed a similar dissociation between VPC, which was associated with strong memories, and DPC, which was associated with weak memories. MTL, PFC, and parietal findings are discussed below.

Medial Temporal Lobes

Consistent with strength theory, the right hippocampus showed greater activity for high- than low-confidence responses during both item and source memory tasks (Figure 2A). This activation is consistent with previous fMRI studies of episodic retrieval that have reported increased activity as a function of memory strength (for a review, see Wais, 2008). For instance, greater hippocampal activity has been observed during high-confidence item recognition, regardless of whether source information was accurate for those item trials (Wais, 2011). Although the hippocampal activation reported by Wais (2011) was bilateral, the activation reported on the right [28 –17 –11] was in a similar location as the current study [34 –23 –8]. Given that high-confidence item memory may reflect recollection, dual-process theorists could argue that the hippocampal activation in Figure 2A reflected a

common recollection component in item and source memory tasks. However, high-confidence item memory may reflect strong recollection and strong familiarity, whereas source memory tasks are considered to primarily rely on recollection (Yonelinas et al., 2010). Thus, in terms of hippocampal activation, dual-process theory would predict a stronger confidence effect for source than item memory.

A stronger confidence effect for source than item memory was in fact found in an adjacent right hippocampal region (Figure 2B). This activation, which extended into parahippocampal cortex, showed a confidence effect in the source memory but not in the item memory task. This activation is consistent with dual-process theory, particularly when considered with the finding of bilateral rhinal regions showing the reverse effect, namely a confidence effect in the item but not in the source memory task (Figure 2C). This double dissociation between the hippocampus and rhinal cortex is difficult to explain in terms of strength theory. According to strength theories, the hippocampal–rhinal dissociations reported in previous fMRI studies can be explained by assuming that the hippocampus is more sensitive to strong memories, whereas rhinal cortex is more sensitive to weak memories (Wais, 2008; Squire et al., 2007). However, this hypothesis predicts that the hippocampus should show greater activity for high- than low-confidence trials in both memory tasks whereas rhinal cortex should show greater activity for low- than high-confidence trials in both tasks, although these hypotheses do not appear to fit the data in Figure 2B and C. Although strength theory makes no direct predictions about the magnitude of confidence effects in an item versus a source task, it cannot easily explain the current pattern of results; that is, why a region in the hippocampus shows a confidence effect for source memory, whereas a region in rhinal cortex shows a confidence effect for item memory.

Our MTL findings provided some support for strength theory, yet the overall pattern of MTL results fits better with dual-process theories. That is, the main effect of confidence observed in the right hippocampal region in Figure 2A is consistent with strength theory, whereas the hippocampal–rhinal dissociation in Figure 2B and C fits better with dual-process theory. One possible way to explain the hippocampal findings would be to argue that some hippocampal subregions are sensitive to overall memory strength, whereas other hippocampal subregions are differentially involved in recollection. However, the two hippocampal activations are so close to each other that a simple anatomical distinction (e.g., anterior vs. posterior, ventral vs. dorsal) cannot account for the different activation patterns. An alternative explanation is the existence of neuronal populations differentially sensitive to strength or to recollection, whose distributions are not homogenous across the hippocampus, leading to different activation patterns within one fMRI study (Figure 2A vs. Figure 2B) and to inconsistencies across different fMRI studies. At any rate, given that functional neuroimaging can only identify whether a region is involved in a task but not whether the region is critical for task performance, the strength versus dual-process debate cannot be reconciled without complementary evidence from patient and animal lesion studies.

Prefrontal Cortex

Comparison of source relative to item memory, collapsed across memory strength, and revealed predominately left-lateralized PFC activity (Figure 3B). Importantly, activity in these left PFC regions was modulated by qualitative rather than quantitative information. Memory strength did not influence activation within these areas, yet qualitatively, they responded preferentially to the type of information to be recalled, namely source memory information. Although the qualitative pattern is consistent with dual-process theory, the lack of a confidence effect in the source memory tasks suggests that these regions are involved in orienting toward recollection or recollective orienting rather than in recollection per se (Kahn et al., 2004; Dobbins et al., 2003; Dobbins et al., 2002). The notion that the

activations in Figure 3B reflect preretrieval orientation is consistent with the results of a study using a cue-probe paradigm that found greater left PFC when participants were preparing to make a source than an item memory decision (cue), even when the actual retrieval probe was not presented (Dobbins & Han, 2006). Thus, the left PFC activations are consistent with a dual-process model assuming qualitatively different processes for recollection. However, in this case, the difference arises because of processes that occur in preparation for recollection rather than processing recollected details. An alternative interpretation is that these left prefrontal regions respond preferentially to successful source retrieval (relative to item retrieval), because the comparison focuses on source hits versus item hits. Nevertheless, both interpretations are consistent with the notion that source versus item retrieval are differentially processed in left PFC.

In contrast with left PFC, right PFC showed a pattern generally consistent with strength theory because it showed greater activity for low than high confidence in both memory tasks. However, this pattern is not necessarily inconsistent with dual-process account because it is likely to reflect retrieval control processes that could apply to both recollection and familiarity. In fact, greater right PFC activity for demanding memory decisions has been attributed to “postretrieval monitoring” processes (Dobbins, Simons, & Schacter, 2004; Henson, Shallice, Rugg, Fletcher, & Dolan, 2001; Henson et al., 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999), that are likely to apply to both recollection and familiarity signals. More generally, there is evidence that the right PFC mediates monitoring processes that are not specific to memory. A study from our laboratory found that some of the same right PFC regions that show greater activity for low-confidence decisions during episodic retrieval also show greater activity for low confidence decisions during a visual perceptual task with no long-term memory component (Fleck et al., 2006). Thus, some right PFC regions seem to be involved in monitoring processes that include but are not limited to monitoring episodic memories.

In summary, whereas greater left PFC activity for source than item memory is more consistent with dual-process theory, greater right PFC activity for low- than high-confidence decisions is more consistent with strength theory. However, rather than recollection per se, the left PFC activations are more likely to reflect an orientation toward recollection, and rather than weak memory processing per se, the right PFC activations are more likely to reflect general monitoring. Thus, it would seem that, to account for PFC activations, dual-process and strength memory theories would need to be expanded and integrated with more general models of PFC-mediated control and decision processes.

Parietal Cortex

Finally, whereas evidence to support dual-process and strength theories was found in MTL and PFC activation patterns, parietal activations patterns were more consistent with strength theory. As predicted by this theory, parietal regions showed similar confidence effects for both item and source memory tasks. In both tasks, VPC showed greater activity for high than low confidence (Figure 3C), whereas DPC showed greater activity for low than high confidence (Figure 3D). These results differ from previous reports, which have linked VPC activity to recollection (Vilberg & Rugg, 2007, 2009; Wagner et al., 2005). In the current paradigm, if VPC was associated with recollection, this region should have shown greater confidence effects (high > low) in the source than in the item memory task, similar to the hippocampal region in Figure 2B. Yet, VPC showed either a main effect of confidence (Figure 3C) or greater confidence effects (high > low) for item than source memory (TPJ: 38–41 27, see Table 2). The latter effect is difficult to fit with a recollection-based interpretation. Although item memory trials, particularly those made with high confidence, are often associated with recollection (Kim & Cabeza, 2009; Daselaar, Fleck, & Cabeza, 2006), source memory relies on recollection to a greater extent than item memory

(Yonelinas et al., 2010), which makes the VPC pattern of activation difficult to attribute to recollection processes alone.

Although strength theory suggests that VPC is involved in processing strong memories and DPC in processing weak memories, it is not clear what specific cognitive operations are mediated by these regions during episodic retrieval. One possible answer to this question is provided by the Attention to Memory model (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008), which postulates that DPC is involved in top-down attention processes during demanding pre- and postretrieval processing, whereas VPC is involved in bottom-up attention processes captured by the retrieval of relevant episodic memories or by salient retrieval cues. Thus, DPC shows greater activity for weak memories because it engages search and monitoring processes dependent on top-down attention, whereas VPC shows greater activity for strong memories because it grabs bottom-up attention. An alternative theoretical account of VPC activity during episodic retrieval is the *episodic buffer hypothesis* (Vilberg & Rugg, 2008), which postulates that VPC is involved in maintaining integrated multimodal information within working memory. Given that the demands for this process can be assumed to be higher for recollection than familiarity, this hypothesis can account for VPC activity during conditions associated with recollection (Vilberg & Rugg, 2008). However, this hypothesis cannot easily account why VPC's sensitivity to confidence in the current study was similar (Figure 3C) or even greater (Table 2) in the item than the source memory condition, when multimodal integration demands were most likely greater in the source condition. The lack of support for the episodic buffer hypothesis could be attributed to the nature of the paradigm used in the current study. A limitation of the current approach is that both source encoding tasks required judgments associated predominately with internal processing: mental imagery associated with a size judgment or assessment of internal valence. A source encoding task that relied more heavily on multimodal integration or allocated more time for deeper encoding may have resulted in enhanced VPC activity for high-confidence source relative to item trials.

In summary, parietal findings were better explained by a strength account: DPC with processing weak memories whereas VPC was associated with processing strong memories. The specific cognitive operations contributed by these regions to the processing of strong versus weak memories can be inferred from parietal models such as the Attention to Memory account, which links DPC to top-down attention and VPC to bottom-up attention.

Conclusions

The current findings provide support for both dual-process and strength theories of episodic memory. Within MTL, the different confidence effects observed in the hippocampus versus rhinal cortex was most consistent with dual-process theory. Within PFC, the left PFC activations were more consistent with dual-process theory whereas the right PFC activations were more consistent with strength theory. However, to account for the specific activation patterns in this and other studies, one must link these theories to more general accounts of PFC-mediated control processes. Finally, parietal activations were consistent with strength theory, as both tasks showed low-confidence activity in DPC but high-confidence activity in VPC. Yet, the specific cognitive operations contributed by these regions are better characterized in terms of attention processes, rather than memory processes per se. The present results suggest that both dual-process and strength theories are partly correct, highlighting the need for an integrated model that links to more general cognitive theories to account for neural activity during episodic retrieval.

Acknowledgments

The authors thank Michael White and Micah Adams for assistance with data collection and Allen Song for providing technical assistance with MRI data acquisition. We would also like to thank two anonymous reviewers for their helpful comments. This work was supported by the National Institutes of Health, the National Institute on Aging (NIA; grants R01 AG019731 and R56 AG23770 awarded to R. C. and grant F32 AG029738 awarded to S. M. H.) and the Department of Veterans Affairs, Veterans Health Administration, Rehabilitation Research & Development Service (grant E7822W awarded to S. M. H.). The content is solely the responsibility of the authors and does not necessarily represent the official views of NIH or NIA.

REFERENCES

- Aggleton JP, Brown MW. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*. 1999; 22:425–489. [PubMed: 11301518]
- Ally BA, Simons JS, McKeever JD, Peers PV, Budson AE. Parietal contributions to recollection: Electrophysiological evidence from aging and patients with parietal lesions. *Neuropsychologia*. 2008; 46:1800–1812. [PubMed: 18402990]
- Berryhill ME, Phuong L, Picasso L, Cabeza R, Olson IR. Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *Journal of Neuroscience*. 2007; 27:14415–14423. [PubMed: 18160649]
- Buchler NG, Light LL, Reder LM. Memory for items and associations: Distinct representations and processes in associative recognition. *Journal of Memory and Language*. 2008; 59:183–199. [PubMed: 18677424]
- Cabeza R. Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia*. 2008; 46:1813–1827. [PubMed: 18439631]
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M. The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*. 2008; 9:613–625.
- Cabeza R, Locantore JK, Anderson ND. Lateralization of prefrontal activity during episodic memory retrieval: Evidence for the production-monitoring hypothesis. *Journal of Cognitive Neuroscience*. 2003; 15:249–259. [PubMed: 12676062]
- Cabeza R, Nyberg L. Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*. 2000; 12:1–47. [PubMed: 10769304]
- Ciaramelli E, Grady CL, Moscovitch M. Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*. 2008; 46:1828–1851. [PubMed: 18471837]
- Coltheart M. The MRC psycholinguistic database. *The Quarterly Journal of Experimental Psychology: Section A*. 1981; 33:497–505.
- Daselaar SM, Fleck MS, Cabeza R. Triple dissociation in the medial-temporal lobes: Recollection, familiarity, and novelty. *Journal of Neurophysiology*. 2006; 96:1902–1911. [PubMed: 16738210]
- Davachi L, Mitchell JP, Wagner AD. Multiple routes to memory: Distinct medial-temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences, U.S.A.* 2003; 100:2157–2162.
- Davidson PSR, Anaki D, Ciaramelli E, Cohn M, Kim ASN, Murphy KJ, et al. Does lateral parietal cortex support episodic memory?: Evidence from focal lesion patients. *Neuropsychologia*. 2008; 46:1743–1755. [PubMed: 18313699]
- Diana RA, Yonelinas AP, Ranganath C. Imaging recollection and familiarity in the medial-temporal lobe: A three-component model. *Trends in Cognitive Sciences*. 2007; 11:379–386. [PubMed: 17707683]
- Dobbins IG, Foley H, Schacter DL, Wagner AD. Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron*. 2002; 35:989–996. [PubMed: 12372291]
- Dobbins IG, Han S. Cue- versus probe-dependent prefrontal cortex activity during contextual remembering. *Journal of Cognitive Neuroscience*. 2006; 18:1439–1452. [PubMed: 16989546]
- Dobbins IG, Rice HJ, Wagner AD, Schacter DL. Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia*. 2003; 41:318–333. [PubMed: 12457757]

- Dobbins IG, Simons JS, Schacter DL. fMRI evidence for separable and lateralized prefrontal memory monitoring processes. *Journal of Cognitive Neuroscience*. 2004; 16:908–920. [PubMed: 15298779]
- Duarte A, Ranganath C, Knight RT. Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience*. 2005; 25:8333–8337. [PubMed: 16148241]
- Eichenbaum H, Yonelinas AP, Ranganath C. The medial-temporal lobe and recognition memory. *Annual Review of Neuroscience*. 2007; 30:123–152.
- Fleck MS, Daselaar SM, Dobbins IG, Cabeza R. Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cerebral Cortex*. 2006; 16:1623–1630. [PubMed: 16400154]
- Hayes SM, Ryan L, Schnyer DM, Nadel L. An fMRI study of episodic memory: Retrieval of object, spatial, and temporal information. *Behavioral Neuroscience*. 2004; 118:885–896. [Article]. [PubMed: 15506871]
- Henson R, Shallice T, Rugg M, Fletcher P, Dolan R. Functional imaging dissociations within right prefrontal cortex during episodic memory retrieval. *Brain and Cognition*. 2001; 47:79–81.
- Henson RNA, Rugg MD, Shallice T, Dolan RJ. Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience*. 2000; 12:913–923. [PubMed: 11177413]
- Henson RNA, Rugg MD, Shallice T, Josephs O, Dolan RJ. Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*. 1999; 19:3962–3972. [PubMed: 10234026]
- Jacoby LL. A process dissociation framework—Separating automatic from intentional uses of memory. *Journal of Memory and Language*. 1991; 30:513–541.
- Janowsky JS, Shimamura AP, Squire LR. Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia*. 1989; 27:1043–1056. [PubMed: 2797412]
- Johnson MK, O'Connor M, Cantor J. Confabulation, memory deficits, and frontal dysfunction. *Brain and Cognition*. 1997; 34:189–206. [PubMed: 9220085]
- Kahn I, Davachi L, Wagner AD. Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience*. 2004; 24:4172–4180. [PubMed: 15115812]
- Kim H, Cabeza R. Common and specific brain regions in high- versus low-confidence recognition memory. *Brain Research*. 2009; 1282:103–113. [PubMed: 19501072]
- Kirwan CB, Wixted JT, Squire LR. Activity in the medial-temporal lobe predicts memory strength, whereas activity in the prefrontal cortex predicts recollection. *Journal of Neuroscience*. 2008; 28:10541–10548. [PubMed: 18923030]
- Kucera, H.; Francis, WN. Computational analysis of present-day American English. Brown University Press; Providence, RI: 1967.
- Maldjian JA, Laurienti PJ, Burdette JH. Precentral gyrus discrepancy in electronic versions of the Talairach atlas. *Neuroimage*. 2004; 21:450–455. [PubMed: 14741682]
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage*. 2003; 19:1233–1239. [PubMed: 12880848]
- Mandler G. Recognizing—The judgment of previous occurrence. *Psychological Review*. 1980; 87:252–271.
- Mickes L, Wais PE, Wixted JT. Recollection is a continuous process: Implications for dual-process theories of recognition memory. *Psychological Science*. 2009; 20:509–515. [PubMed: 19320859]
- Mitchell KJ, Johnson MK. Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin*. 2009; 135:638–677. [PubMed: 19586165]
- Olson IR, Berryhill M. Some surprising findings on the involvement of the parietal lobe in human memory. *Neurobiology of Learning and Memory*. 2009; 91:155–165. [PubMed: 18848635]
- Pruessmann KP, Weiger M, Bornert P, Boesiger P. Advances in sensitivity encoding with arbitrary k-space trajectories. *Magnetic Resonance in Medicine*. 2001; 46:638–651. [PubMed: 11590639]

- Ranganath C, Yonelinas AP, Cohen MX, Dy CJ, Tom SM, D'Esposito M. Dissociable correlates of recollection and familiarity within the medial-temporal lobes. *Neuropsychologia*. 2004; 42:2–13. [PubMed: 14615072]
- Rorden C, Brett M. Stereotaxic display of brain lesions. *Behavioural Neurology*. 2000; 12:191–200. [PubMed: 11568431]
- Shimamura AP, Janowsky JS, Squire LR. Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia*. 1990; 28:803–813. [PubMed: 2247207]
- Shrager Y, Kirwan CB, Squire LR. Activity in both hippocampus and perirhinal cortex predicts the memory strength of subsequently remembered information. *Neuron*. 2008; 59:547–553. [PubMed: 18760691]
- Simons JS, Peers PV, Hwang DY, Ally BA, Fletcher PC, Budson AE. Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*. 2008; 46:1185–1191. [PubMed: 17850832]
- Simons JS, Peers PV, Mazuz YS, Berryhill ME, Olson IR. Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*. 2010; 20:479–485. [PubMed: 19542474]
- Simons JS, Verfaellie M, Galton CJ, Miller BL, Hodges JR, Graham KS. Recollection-based memory in frontotemporal dementia: Implications for theories of long-term memory. *Brain*. 2002; 125:2523–2536. [PubMed: 12390977]
- Skinner EI, Fernandes MA. Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia*. 2007; 45:2163–2179. [PubMed: 17445844]
- Slotnick, SD. [July 26, 2010] Cluster threshold. 2010. from www2.bc.edu/~slotnics/scripts.htm
- Squire LR, Wixted JT, Clark RE. Recognition memory and the medial-temporal lobe: A new perspective. *Nature Reviews Neuroscience*. 2007; 8:872–883.
- Truong TK, Song AW. Single-shot dual-z-shimmed sensitivity-encoded spiral-in/out imaging for functional MRI with reduced susceptibility artifacts. *Magnetic Resonance in Medicine*. 2008; 59:221–227. [PubMed: 18050341]
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, et al. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*. 2002; 15:273–289. [PubMed: 11771995]
- Vilberg KL, Rugg MD. Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*. 2007; 45:2216–2225. [PubMed: 17449068]
- Vilberg KL, Rugg MD. Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*. 2008; 46:1787–1799. [PubMed: 18343462]
- Vilberg KL, Rugg MD. Functional significance of retrieval-related activity in lateral parietal cortex: Evidence from fMRI and ERPs. *Human Brain Mapping*. 2009; 30:1490–1501. [PubMed: 18649352]
- Wager TD, Nichols TE. Optimization of experimental design in fMRI: A general framework using a genetic algorithm. *Neuroimage*. 2003; 18:293–309. [PubMed: 12595184]
- Wagner AD, Shannon BJ, Kahn I, Buckner RL. Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*. 2005; 9:445–453. [PubMed: 16054861]
- Wais PE. fMRI signals associated with memory strength in the medial-temporal lobes: A meta-analysis. *Neuropsychologia*. 2008; 46:3185–3196. [PubMed: 18817791]
- Wais PE. Hippocampal signals for strong memory when associative memory is available and when it is not. *Hippocampus*. 2011; 21:9–21. [PubMed: 20014387]
- Wais PE, Squire LR, Wixted JT. In search of recollection and familiarity signals in the hippocampus. *Journal of Cognitive Neuroscience*. 2010; 22:109–123. [PubMed: 19199424]
- Wixted JT. Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*. 2007; 114:152–176. [PubMed: 17227185]
- Wixted JT, Mickes L, Squire LR. Measuring recollection and familiarity in the medial-temporal lobe. *Hippocampus*. 2010; 20:1195–1205. [PubMed: 20848603]

- Yonelinas AP. Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1994; 20:1341–1354.
- Yonelinas AP. The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*. 2002; 46:441–517. [Review].
- Yonelinas AP, Aly M, Wang WC, Koen JD. Recollection and familiarity: Examining controversial assumptions and new directions. *Hippocampus*. 2010; 20:1178–1194. [PubMed: 20848606]

\$watermark-text

\$watermark-text

\$watermark-text

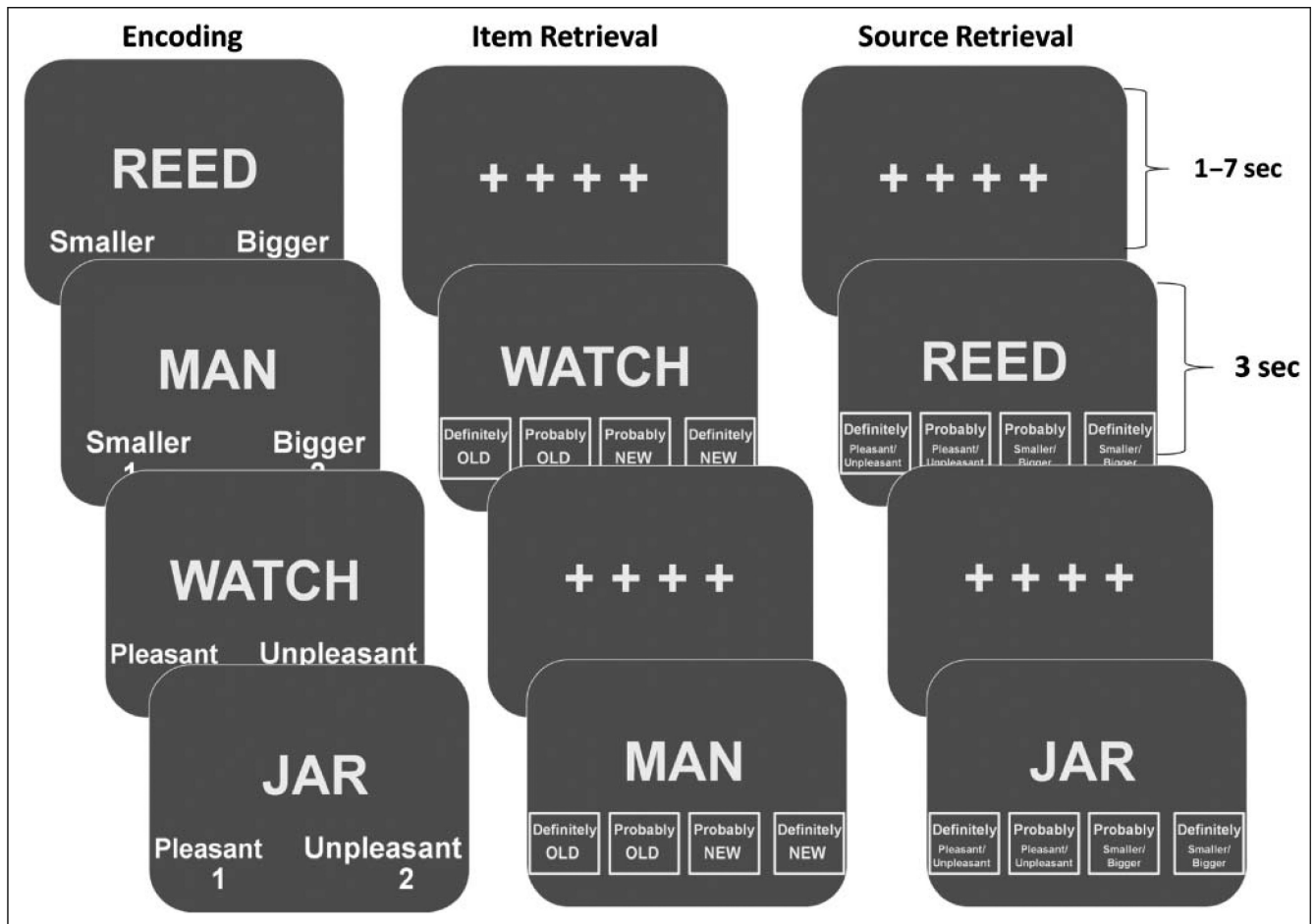


Figure 1.

Experimental design. Participants made smaller/bigger than a shoebox or pleasant/unpleasant judgments during encoding, which occurred before the MRI session. During item retrieval, participants made old/new judgments on a 4-point scale (definitely old, probably old, probably new, definitely new). During source retrieval, participants made source judgments on a 4-point scale. During fMRI scanning, stimuli were presented for 3 sec with a jittered ISI (represented by ++++).

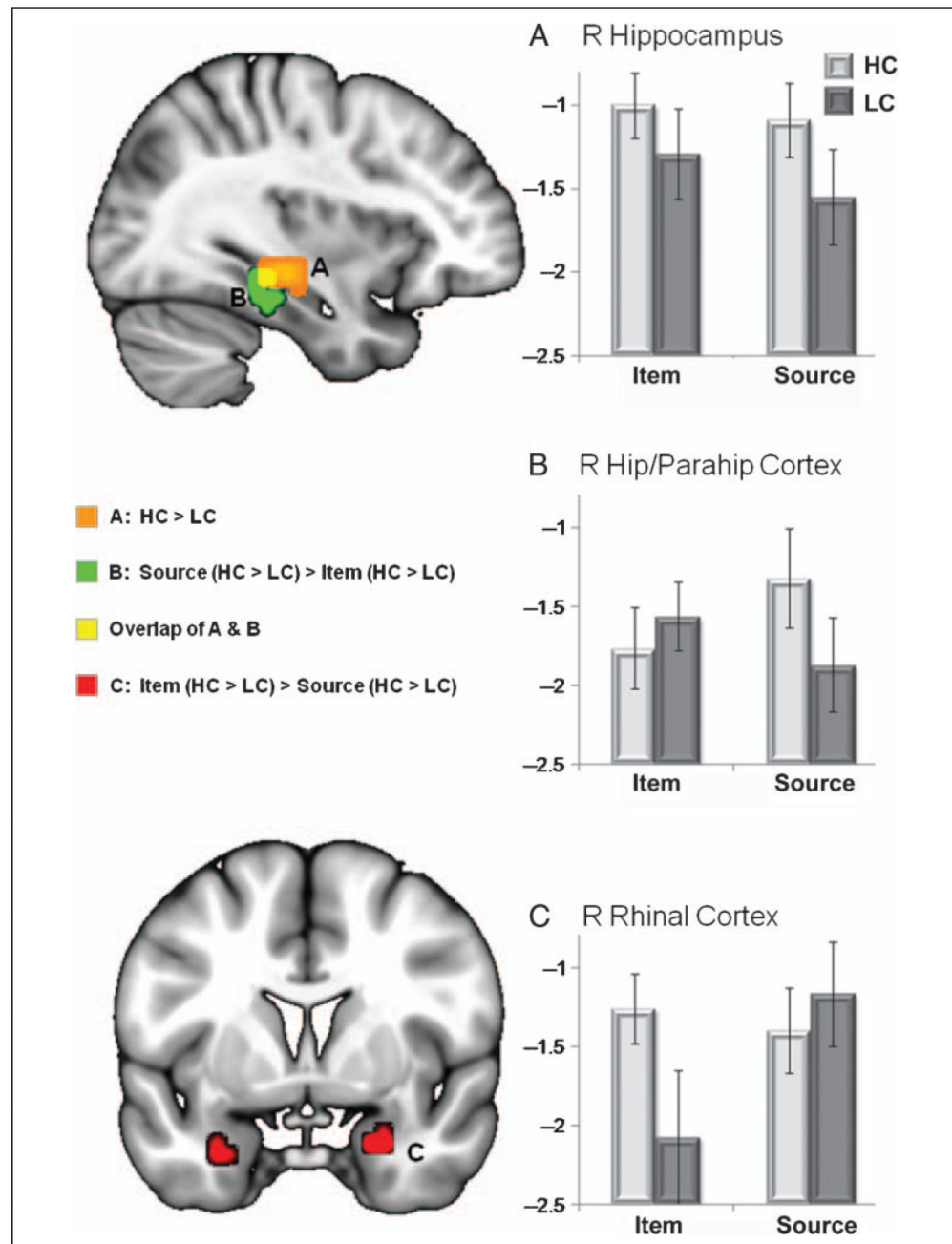


Figure 2.

The MTLs showed evidence of both a quantitative and qualitative response. The *y* axis reflects the fMRI effect size (parameter estimate or beta weight) with error bars representing the *SEM*. (A) The main effect of memory strength, high > low confidence, collapsed across task, in the hippocampus [30 -23 -8]. (B) The confidence effect during source retrieval, source (high > low confidence) > item (high > low confidence), in an adjacent hippocampal/parahippocampal region [34 -34 -11]. The overlap of A and B is represented in yellow and occurs primarily within the hippocampus. (C) Confidence effects during item recognition, item (high > low confidence) > source (high > low confidence), in bilateral rhinal cortex [-30 0 -31 ; 23 4 -27]. Hip/Parahip = hippocampus/parahippocampal; HC = high confidence; LC = low confidence; R = right.

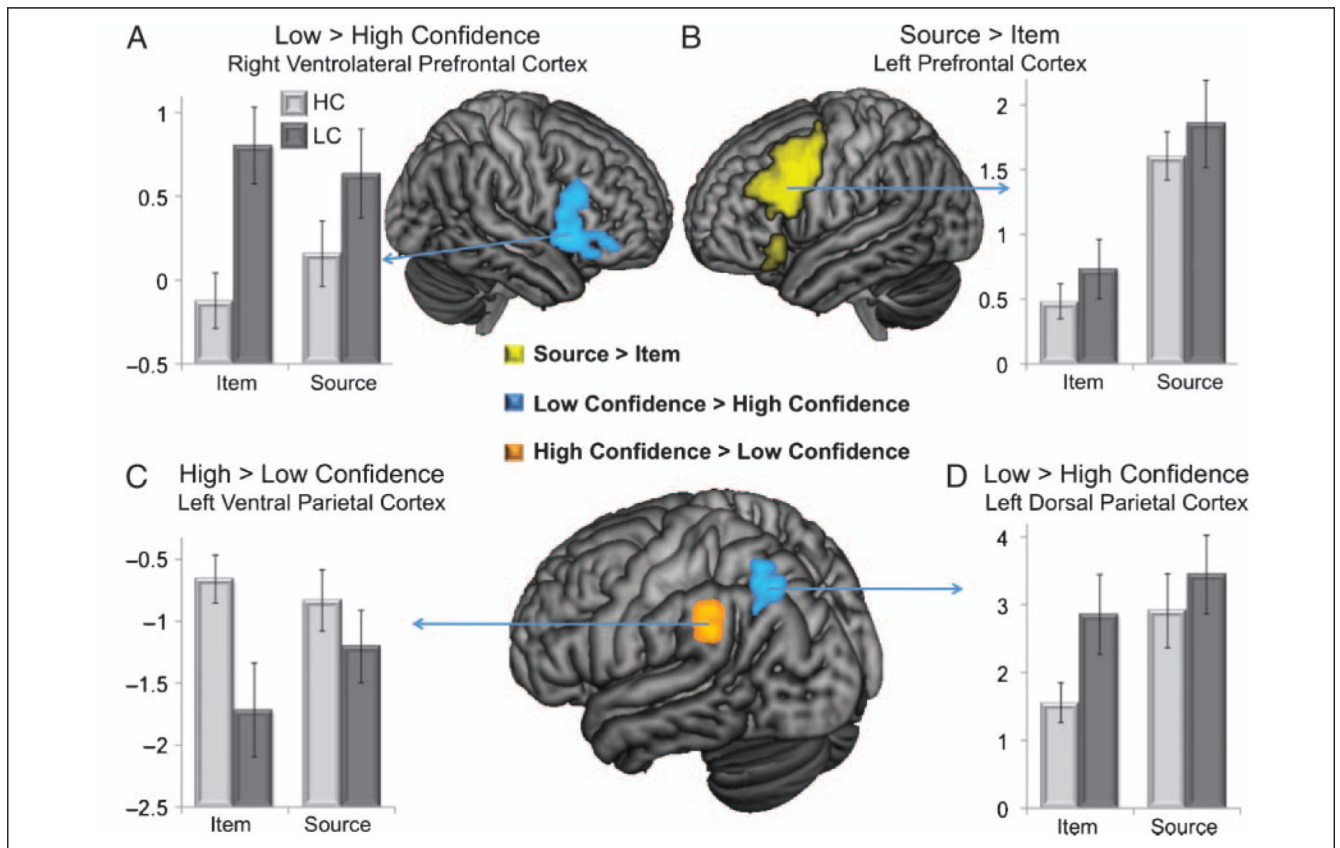


Figure 3.

Quantitative and qualitative activity in prefrontal and parietal cortex. The y axis reflects the fMRI effect size (parameter estimate or beta weight) with error bars representing the SEM . (A) Within PFC, analysis of quantitative differences in episodic memory retrieval revealed right ventrolateral PFC activity in low > high confidence memory (blue activation: 38 11 – 4). (B) Analysis of qualitative differences, source > item collapsed across confidence, revealed predominately left-lateralized PFC activity (yellow activation, peak MNI coordinates: –38 11 38). (C, D) The observed dissociation in parietal cortex, as VPC activity was associated with high > low confidence memory reflecting bottom–up capture of attention by memory (C, orange activation: –45 –45 30), whereas increased DPC activity was observed for low > high confidence responses (D, blue activation: –19 –68 46), supporting increased top–down attention for effortful memory search. Brain activity of primary interest is highlighted in these figures. See Table 2 for the complete list of brain regions active for each contrast. HC = high confidence, LC = low confidence.

Table 1Mean Accuracy (*SD*) for the Item and Source Memory Tasks

	Low Confidence	High Confidence	Total
Item Hit Rate	.19 (.12)	.70 (.16)	.89 (.07)
Item False Alarms	.15 (.10)	.08 (.05)	.23 (.13)
Item Corrected Recognition	.04 (.13)	.62 (.14)	.66 (.16)
Source Hit Rate	.36 (.14)	.47 (.17)	.83 (.10)
Source False Alarms	.13 (.08)	.05 (.05)	.18 (.10)
Source Corrected Recognition	.23 (.14)	.42 (.17)	.65 (.20)

Table 2

Results of ROI and Whole-brain Analyses

Contrast/Brain Region	L/R	BA	MNI Coordinates				
			x	y	z	k	t
<i>High > Low Confidence</i>							
Hippocampus	R		30	-23	-8	6	3.12 ^a
Amygdala/rhinal cortex	R		19	0	-15	32	3.75 ^a
	L		-19	0	-11	53	3.43 ^a
VPC: supramarginal gyrus	L	40	-45	-45	30	47	3.42
	L	40	-53	-49	45	47	3.09
Precuneus/cuneus	R	31/18	4	-79	23	172	3.98
Cuneus	L	17	-11	-79	26	172	3.63
Posterior cingulate cortex	L	31	-11	-45	42	67	3.68
Paracentral lobule	M	5	0	-38	53	67	2.98
Fusiform gyrus	R		45	-26	-30	13	2.85 ^a
Middle temporal gyrus	L	21	-64	-30	-15	59	3.37
Putamen	L		-19	4	-8	184	3.82
Nucleus accumbens	R		11	11	-11	184	3.77
<i>Low > High Confidence</i>							
Rhinal cortex	R		30	-4	-38	13	2.84 ^a
PFC: Ventrolateral/insula	R	45/47	38	11	-4	161	4.65
	R	47	45	19	-4	161	4.19
	R	45	53	23	27	161	3.35
Dorsal parietal cortex	R	7	15	-68	53	32	3.98
Precuneus	L	7	-19	-68	46	37	3.42
Precuneus	L	7	-19	-60	57	37	2.92
PFC: dorsolateral	L	9	-41	8	38	57	3.48
Fusiform gyrus	R		26	-45	-15	15	2.63 ^a
	R		26	-83	-4	11	3.03 ^a

Contrast/Brain Region	L/R	BA	MNI Coordinates				
			x	y	z	k	t
Cingulate gyrus	M	32/24	-4	15	42	386	4.42
Precentral gyrus	L	4	-26	-15	68	386	4.66
Cuneus	R	17/18	4	-94	4	206	4.3
	R	18	19	-90	0	206	3.62
	L	18	-23	-90	-3	206	3.57
Thalamus	L		-49	4	49	38	3.94
Source (High > Low Confidence) > Item (High > Low Confidence)							
Hippocampus	R		34	-34	-11	8	2.04 ^a
Fusiform gyrus	L		-45	-56	-15	8	3.00
	L		-38	-41	23	16	2.46 ^a
	R		34	-64	-11	5	2.50 ^a
Postcentral gyrus	L	43	-52	-15	27	10	3.75
Inferior temporal gyrus	L	20	-45	-15	-27	11	3.43
Item (High > Low Confidence) > Source (High > Low Confidence)							
Rhinal cortex	L		-30	0	-31	5	2.76 ^a
	R		23	4	-27	6	2.45 ^a
VPC: temporo-parietal junction	L	40	-38	-41	27	17	2.98
Caudate nucleus	R		22	0	19	13	3.51
	L		-8	8	19	52	3.17
Source > Item							
PFC: dorsolateral	L	8/9	-38	11	38	387	5.20
Dorsolateral	L	9/44	-38	15	30	387	5.09
	L	8/6	-38	15	52	387	4.54
Ventrolateral	L	47	-45	26	-8	38	3.47
Anterior	L	10	-23	60	15	34	3.65
Medial	L	8	-8	34	53	131	3.94
	L	8	-4	15	57	131	3.68
	R	8	8	30	49	131	3.56
Dorsolateral	R	9	45	19	38	43	3.64

Contrast/Brain Region	L/R	BA	MNI Coordinates				k	t
			x	y	z			
Inferior parietal lobule	L	7	-30	-60	46	319	4.49	
Precuneus	L	7	-8	-68	49	319	4.07	
	L	7	-22	-71	53	319	3.88	
Middle temporal gyrus	L	21	-60	-41	-4	73	4.42	
	L	21	-53	-45	3	73	3.77	
Calcarine sulcus	M	17	0	-90	0	85	3.80	

A maximum of three subpeaks are reported for each cluster.
L = left, R = right, M = midline, k = voxel extent, t = t value, BA = Brodmann Areas, VPC = ventral parietal cortex.
^aROI.