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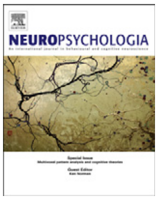

Encoding-related brain activity dissociates between the recollective processes underlying successful recall and recognition: A subsequent-memory study

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ABSTRACT

The subsequent-memory (SM) paradigm uncovers brain mechanisms that are associated with mnemonic activity during encoding by measuring participants' neural activity during encoding and classifying the encoding trials according to performance in the subsequent retrieval phase. The majority of these studies have converged on the notion that the mechanism supporting recognition is mediated by familiarity and recollection. The process of recollection is often assumed to be a recall-like process, implying that the active search for the memory trace is similar, if not identical, for recall and recognition. Here we challenge this assumption and hypothesize – based on previous findings obtained in our lab – that the recollective processes underlying recall and recognition might show dissociative patterns of encoding-related brain activity. To this end, our design controlled for familiarity, thereby focusing on contextual, recollective processes. We found evidence for dissociative neurocognitive encoding mechanisms supporting subsequent-recall and subsequent-recognition. Specifically, the contrast of subsequent-recognition versus subsequent-recall revealed activation in the Parahippocampal cortex (PHc) and the posterior hippocampus—regions associated with contextual processing. Implications of our findings and their relation to current cognitive models of recollection are discussed.

1. Introduction

The subsequent-memory (SM) paradigm (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980; Wagner et al., 1998) has greatly advanced our understanding of the brain mechanisms underlying encoding of to-be-remembered episodic information. In the SM paradigm, participants' neural activity is measured during encoding and the encoding trials are classified according to performance in the subsequent retrieval phase. This paradigm, therefore, uncovers brain mechanisms that are associated with mnemonic activity during encoding.

The vast majority of SM studies probed memory with recognition tests (Spaniol et al., 2009). These studies have converged, together with a plethora behavioral evidence (Yonelinas, 2002), on the notion that two different processes mediate recognition: familiarity and recollection (for a review see Diana, Yonelinas, & Ranganath, 2007). Familiarity is an automatic process which is associated to the fluency with which an item is processed—with studied items processed more fluently than unstudied items (Whittlesea & Leboe, 2000). In contrast, recollection is a strategic, conscious process which involves reinstatement of the memory trace within its context (Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005; Yonelinas, 2002). Whereas familiarity is a process unique to recognition, recollection is viewed as a ”recall-like” process, wherein an active search for the memory trace takes place (e.g., Dunn, 2008; Guderian, Brigham, & Mishkin, 2011; Humphreys et al., 2010; Rotello & Heit, 2000; Yonelinas, 1997).

Importantly, an underlying assumption of the view that the recollection component of recognition is a recall-like process is that the active search for the memory trace is similar, if not identical, for recall and recognition. Recently, we have provided evidence against this view, by showing that the recollective processes underlying recognition and recall are supported by dissociative neurocognitive mechanisms during retrieval (Sadeh et al., 2011). This dissociation was manifested in differential patterns of interactions between Medial Temporal Lobe (MTL) structures during tests of recognition and recall. In the current study, we asked whether we can find further evidence for this dissociation by examining the MTL encoding mechanisms supporting recollection-based recognition and recall. Thus, we capitalize on the SM paradigm to investigate whether the encoding process supporting successful recollection in recognition can be

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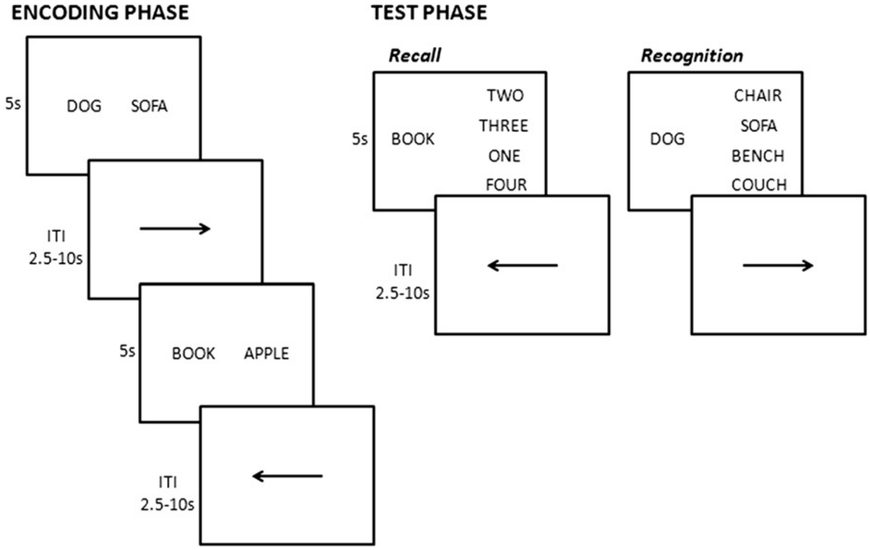

Fig. 1. Stimuli and timing of events. During the encoding phase, participants incidentally studied cue-target word pairs by creating a detailed, bizarre mental image of the two words. The purpose of the words "ONE", "TWO", "THREE", "FOUR" in the recall test, presented in a different random order in each trial, was to equate the visual display with that of the recognition test and to signal to participants to recall the target word. Foils in the recognition test were semantically-similar to the target. During baseline trials (ITIs), participants were required to press one of two keys according to the direction of arrows, randomly pointing left or right.

dissociated from that supporting successful recollection in recall. Importantly, in retrieval, different task demands and a different visual display could hypothetically account for observed differences in neural activity across the memory tests. Critically, such differences cannot account for a dissociative pattern that may be uncovered during the earlier encoding phase, where memory had not yet been probed. Therefore, the SM paradigm allows for a conceptually "cleaner" comparison between tests of recall and recognition.

To date, three studies have compared encoding activity predictive of recall and recognition (Brassen, Weber-Fahr, Sommer, Lehmbeck, & Braus, 2006; Habib & Nyberg, 2008; Staresina & Davachi, 2006). Still, all three assumed that tests of recall differ quantitatively from those of recognition, by requiring more processing. Thus, these studies asked which *additional* encoding resources are needed to successfully recall an item, rather than to merely recognize it. Given this goal, the same set of words were submitted to both recall and recognition tests and the comparison of interest was of words that were both recalled and recognized versus words that were only recognized. In contrast, we argue that recollection-based recognition and recall may differ qualitatively and therefore wished to find unique brain regions which are associated with encoding supporting recollection-based recognition and those that are associated with encoding supporting recall. To this end, each participant had to recall and recognize non-overlapping sets of words. Most importantly, while previous studies capitalized on seeking for brain regions which show a greater SM effect for recall than for recognition, our primary goal was to test for the opposite contrast—namely, test for regions which show a greater SM effect for recognition than for recall.

Critically, because our goal was to compare to recall with the recollection component of recognition, it was essential to entirely eliminate the familiarity component of recognition, thereby leaving only the recollective component to influence performance. Only by eliminating the influence of familiarity, was it possible to determine whether the recollective component mediating recognition can be dissociated from that mediating recall.

To eliminate the effects of familiarity, we used a variant of an associative-recognition paradigm which has been shown to rely only on recollection (Yonelinas, 1997). In our paradigm, study materials consisted of cue-target word pairs. During recognition, participants were presented with a cue and were asked to identify its corresponding target among a set of foils—namely, words which had not been paired with the cue at study. In our variant of the associative-recognition paradigm, we eliminated the influence of familiarity by choosing foils to be words that had appeared earlier in study phase but had been paired with a different cue word. By using such intra-list foils, the familiarity of the individual words that constituted the pairs was equated for targets and foils, thereby eliminating the diagnostic value of familiarity to task performance[1].

Note that as opposed to associative recognition, in yes-no recognition – where participants have to identify the memory status of single items – the foils are, by definition, extra-list items (namely, items which had not been presented at study). Thus, in yes–no recognition, the familiarity of the foils is necessarily lower than that of the target words. In yes–no recognition, therefore, participants may rely on the higher familiarity of the targets to make recognition judgments (Yonelinas, 2002), with recollection not mediating successful recognition. Our choice of an associative-memory paradigm was driven by the need to control for familiarity-based judgments at recognition, which would not have been possible had we used a yes-no recognition memory paradigm.

We used fMRI to measure participants' neural activity while they incidentally encoded cue-target word pairs (Fig. 1). Each of the encoded pairs was subsequently submitted either to a multiple-choice recognition test or to a cued-recall test—but never to both tests. In the multiple-choice recognition test, the cue was presented alongside the target and three foils, and participants had to select the target. In the cued-recall test, the cue was presented alongside four preset words whose purpose was to signal participants to recall the target word which had been studied together with the cue. Because our a-priori interest was in the MTL, our analysis focused on this particular region. An additional region of a-priori interest was the left inferior prefrontal cortex (iPFC). The left iPFC has been reported to play a

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[1] Recent studies have shown that recognition of item pairs may be governed by familiarity when manipulations that promote unitization of the two items are applied (e.g., Haskins, Yonelinas, Quamme, & Ranganath, 2008). However, our methodology differed markedly from that applied in these previous studies as far as such manipulations are concerned. It therefore seems extremely unlikely that recognition in the current study could have relied on familiarity of unitized pairs.

more important role in encoding supporting recall than recognition (Brassen et al., 2006; Staresina & Davachi, 2006). We, therefore, wished to directly assess whether these previous results were replicated in the current study. Our specific interest in the left iPFC also stemmed from its long-known involvement in encoding to episodic memory. In fact, the most recent review of subsequent-memory studies (Spaniol et al., 2009) reports the left iPFC as the most consistently-detected region.

2. Material and methods

2.1. Participants

Participants were 18 native Hebrew speakers (10 women; ages 21–32 years, mean 24.7). Data from four additional participants were excluded due to poor task compliance or excessive motion. All participants were neurologically-intact, right-handed and with normal or corrected-to-normal vision. Experimental procedures were approved by the Tel-Aviv Medical Center's Helsinki committee. Informed consent was obtained in a manner approved by the Tel-Aviv Medical Center on Clinical Investigation.

2.2. Procedure and materials

Recall tests are invariably more difficult than recognition tests (Haist, Shimamura, & Squire, 1992). Therefore, examining recognition and recall within the same study while intermixing items subsequently submitted to each test, likely results in a floor effect in recall. To obtain a sufficient number of raw "Remembered" items in recall – necessary for performing an SM analysis – we introduced systematic differences between recall and recognition, as described in the next paragraph. These differences have all been implemented in the past (e.g., Cabeza et al., 1997; Dennis et al., 2008; Hirst, Johnson, Phelps, & Volpe, 1988), with the explicit goal of controlling for differences in difficulty between memory tests—a frequent confound which retards our ability to compare recognition and recall. In the Discussion we address the possible effects of the systematic differences we introduced vis-à-vis the inherent differences in difficulty between recall and recognition.

To control for differences in difficulty between recognition and recall and avoiding a floor effect in recall, we took the following steps. First, we interposed a longer interval between study and test phases for recognition as compared to recall; at encoding, words to-be-subsequently tested in recognition were studied before those to-be-subsequently tested in recall. Second, the recognition test was preceded by the recall test and by a 20-min distractor task in which English anagrams were solved. Finally, more items were presented in recall than in recognition. Critically, none of the differences we introduced has been found to interact with the mechanisms thought to mediate the search for the memory engram—namely, the recollective mechanism (Cabeza et al., 1997; Hirst et al., 1988).

Stimuli consisted of 200 semantically-unrelated Hebrew cue-target noun pairs. Of the 200 pairs, 120 were used for recall and 80 for recognition. Materials were rotated such that each pair appeared for 40% of the participants in the recognition test and for 60% of the participants in the recall test. For recognition, the cue was presented alongside its target and three additional study-targets (ordered in random positions) thereby equating familiarity of the test foils. The foils were of the same semantic category as the target[2]. To this end, the 200 noun pairs were divided into 50 sets of four pairs such that the four targets in each set were of the same semantic category. Thus, during the multiple-choice test, each target was presented with its three semantically-matched targets four times, each time in a different, random order—once alongside its corresponding cue and the three times alongside each of the three cues corresponding to the other targets in the set (thus serving as a foil).

Each encoding trial consisted of the presentation of a word pair in the center of the screen for 4.5 s followed by a fixation crosshair for 0.5 s. To control for possible differences in encoding strategies and to ensure that studied items were not rehearsed during baseline trials, we used an incidental encoding task. Thus, participants were asked to form a detailed, bizarre mental image of the two words together—manipulations known to enhance memory performance (McDaniel, Einstein, DeLosh, May, & Brady, 1995). The recall and recognition tests were also performed in the scanner, for goals extraneous to those of the present endeavor. The retrieval results are reported in Sadeh et al., 2011.

Instructions for the retrieval phase were presented on the screen, and participants could browse the instructions (proceeding to the next page or going back to the previous page) by pressing the buttons of the response box. In addition, the experimenter confirmed that the instructions were fully comprehended by speaking to the participants through the intercom. Following the instructions, participants were given a short practice session of the memory tests. Instructions and practice were given for recognition and recall separately, prior to presentation of the test itself. For both tests, each trial lasted 5 s. To avoid speech-related motion artifacts, participants indicated their verbal responses using a covert-speech method (for more details see supplementary data) which was validated in extensive pilot studies. As an incentive to enhance performance, participants were told that they would be awarded monetary prizes (comparable to $200) if they reached the highest scores in the experiment.

Baseline trials were interleaved among experimental trials using a rapid event-related design (Dale, 1999). The duration of the baseline trials varied randomly between 2.5 and 10 s, with their total duration equaling one third of the duration of each phase. Traditional passive baseline tasks (fixating on a crosshair) possibly involve mnemonic processing and thus may mask out the effects of interest. Therefore, we used an active baseline task (Staresina & Davachi, 2006; Stark & Squire, 2001), in which participants judged the direction of arrows, randomly pointing left or right. During the baseline task, each arrow appeared on the screen for 1100 ms, followed by a fixation cross for 150 ms, which was then replaced by the next arrow. Because the duration of the baseline trials was between 2.5 and 10 s, in each trial at least two (and at most eight) arrows were presented.

The order and timing of experimental and baseline trials was determined using optseq (http://www.surfer.nmr.mgh.harvard.edu/optseq).

2.3. Imaging procedure & data analysis

Participants were scanned on a GE 3T Signa Horizon LX 9.1 echo speed scanner (Milwaukee, WI). The encoding phase included one scanning session in which items subsequently submitted to recognition were presented and two scanning sessions in which items subsequently submitted to recall were presented. Whole-brain $T2^*$-weighted EPI functional images were acquired (TR = 2500 ms, 20-mm FOV, 64 × 64 matrix, flip angle = 85, TE = 35, 44 pure axial slices, 3-mm thickness; interleaved acquisition order). For the subsequent-recognition scan, 200 volumes were acquired. For each of the two subsequent-recall scans, 150 volumes were acquired. Four additional volumes

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[2] Because our pilot data indicate that at recall many intrusions were of words of the same semantic categories as the target items, the intra-list foils at recognition were of the same semantic categories as the targets.

were acquired at the beginning of each session to allow for T1 equilibration (and were excluded from the analysis).

Imaging data were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London). A slice-timing correction to the first slice was performed followed by realignment of the images. Data was spatially normalized to an EPI template based upon the MNI305 stereotactic space (Cocosco, Kollokian, Kwan, & Evans, 1997). The images were resampled into 2-mm cubic voxels, and smoothed with an 8-mm FWHM isotropic Gaussian kernel.

Encoding trials, for both recall and recognition, were classified into four categories, according to participants' responses in the SM tests: (1) trials for which the correct target was subsequently-retrieved (''Remembered''); (2) trials for which participants subsequently indicated they could not retrieve the target (''Forgotten''); (3) trials for which participants subsequently retrieved an incorrect word (''Wrong''); (4) the remaining trials, including failures to respond and responses made outside the time window (''Other''). Each trial was treated as an event whose duration is two TRs (5 s) and was modeled using a canonical hemodynamic response. For each subject, a fixed-effect model was implemented, with the low-frequency signal component treated as a confound.

Critically, items subsequently submitted to recall ('recall trials') and items subsequently submitted to recognition ('recognition trials') were presented in different scans. Therefore, the first-level model consisted of two sessions, one including the recall trials and the other including the recognition trials. Session effects – which may have otherwise confounded our comparisons of the two tests – were accounted for by regressors that capture the average brain activity per session.

Linear contrasts were used to obtain subject-specific estimates for each of the effects of interest. These estimates were entered into a second-level analysis treating participants as a random effect. Statistical parametric maps were created for the contrasts of interest.

3. Results

3.1. Behavioral

For recognition, a mean of 34 (SE=2.3) targets were Remembered, 27 (SE=2.6) targets were Forgotten and 15 (SE=2.2) were Wrong. For recall, a mean of 26 (SE=2.8) targets were Remembered, 72 (SE=4.5) targets were Forgotten and 17 (SE=2.8) were Wrong. Importantly, the recall data for ''Remembered'' items did not show a floor effect thereby enabling a reliable SM analysis.

3.2. Imaging

All analyses refer to data collected during encoding. In all contrasts, extent threshold is of 5 contiguous voxels.

3.2.1. Encoding task

Performance on the encoding task relied on a variety of cognitive functions including mental imagery, evaluative processes and semantic processing. Accordingly, a whole-brain analysis contrasting activity during all encoding trials versus baseline ($p<0.001$ uncorrected) revealed activation in a number of regions in the temporal cortex, including the left Parahippocampal gyrus (extending to the hippocampus), bilateral Fusiform gyri and the left inferior temporal cortex. In addition, extensive activation was detected in the frontal and parietal cortices (predominantly in the left hemisphere). This pattern of activation is consistent with previous findings (e.g., Staresina & Davachi, 2006).

3.2.2. Contrasting encoding predictive of recall and encoding predictive of recognition

To search for encoding mechanisms which specifically support either recollection-based recognition or recall, we conducted a 2×2 analysis of variance (ANOVA) with memory test (recognition, recall) and condition (remembered, forgotten) as within-subject factors. This analysis searched for MTL regions showing a significant interaction between memory test and condition, and was performed within a second level GLM in SPM. The interaction analysis included the following four conditions: recognition remembered, recognition forgotten, recall remembered and recall forgotten. We defined two interaction contrasts on these conditions: (a) regions showing a greater SM effect for recognition than for recall [1; −1; −1; 1]—henceforth the 'recognition > recall contrast'; (b) regions showing a greater SM effect for recall than for recognition [−1; 1; 1; −1]—henceforth the 'recall > recognition contrast'. Note that while contrasts similar to (b) have been previously examined (Brassen et al., 2006; Habib & Nyberg, 2008; Staresina & Davachi, 2006), contrast (a) – namely, a greater SM effect for recognition than for recall – has never been examined.

Because our a-priori interest was in the MTL, we used an anatomical mask to search for effects only within this predesignated region. The mask was created using the anatomical automatic labeling brain atlas (Tzourio-Mazoyer et al., 2002) and the Wake Forest University Pick Atlas Tool and covered the entire MTL area including the bilateral Parahippocampal gyri, Hippocampus, Amygdala, and Fusiform gyri. This masking procedure allowed for a relatively conservative small-volume correction.

The recognition > recall contrast revealed a large cluster of activation (224 voxels) in the right Parahippocampal cortex (PHc), extending to the posterior hippocampus ($p<0.001$; $p=0.005$, small-volume corrected for the MTL region; Fig. 2). In addition, a smaller cluster of activation (24 voxels) was found in the left PHc, also extending to the posterior hippocampus ($p<0.001$ uncorrected). This cluster, however, did not survive a small-volume correction.

For the recall > recognition contrast, the masking procedure did not reveal any statistically-significant activity within the MTL.

In addition to the MTL area, we focused specifically on the left iPFC, which we predicted would show activity in the recall > recognition contrast, based on previous studies (Brassen et al., 2006; Staresina & Davachi, 2006). Also, as mentioned in the introduction, this region has been consistently implicated in episodic encoding (for reviews see Paller & Wagner, 2002; Spaniol et al., 2009). To our knowledge, there is no specific anatomical mask which can be used to define the relevant iPFC region anatomically, as the iPFC is part of a very large brain region, including four different Brodmann regions (Spaniol et al., 2009). We thus defined the left iPFC as an a-priori region consisting of the sphere around the peak coordinates reported – in the most recent review of subsequent-memory – to be most consistently activated (Spaniol et al., 2009; $x=-42$; $y=12$; $z=28$) and extracted parameter estimates from this region. Parameter estimates were extracted for each of the conditions of interest (recognition remembered, recognition forgotten, recall remembered and recall forgotten). This analysis was conducted for both a sphere of 5-mm radius around the peak coordinates and a sphere of 10-mm radius around these coordinates. For both radii, a 2×2 ANOVA with memory test and condition as within-subject factors revealed an interaction in line with our directional hypothesis: a larger SM effect for recall than for recognition. For the 5-mm radius, the interaction was significant ($F=2.28$,

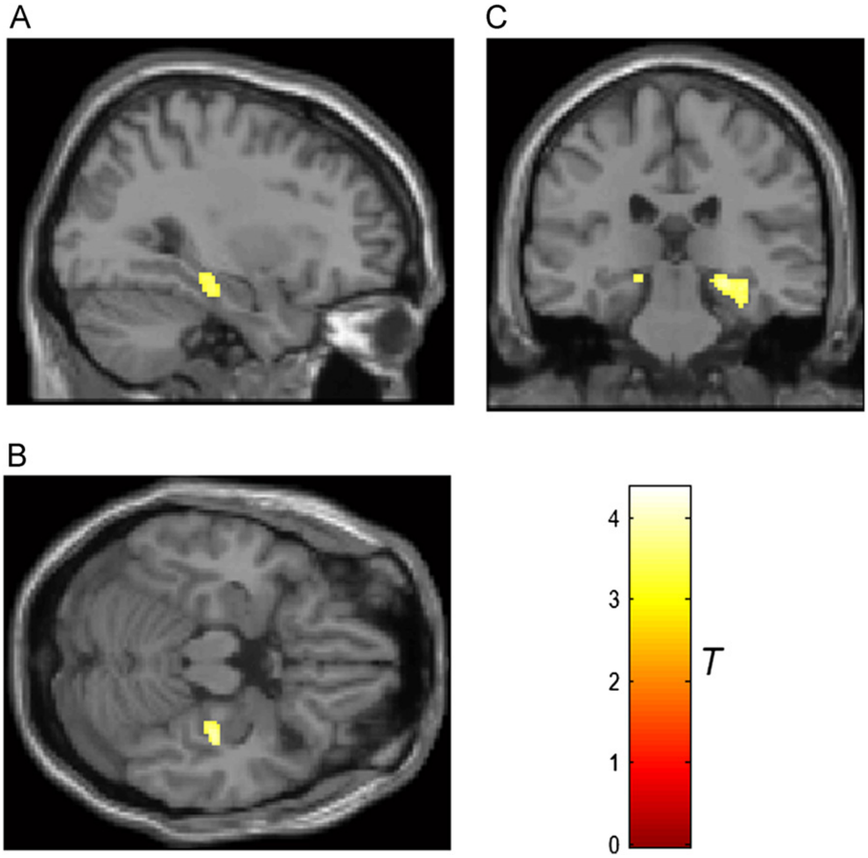

Fig. 2. Right Parahippocampal cortex and posterior hippocampus observed in the recognition > recall contrast. Statistical parametric maps of activation rendered on an average MNI template brain ($p<0.001$, $p=0.005$, small-volume corrected for the MTL region; extent threshold 5 voxels). (A) sagittal view, (B) axial view, (C) coronal view.

$p=0.037$, MSE $=0.098$), and for the 10-mm radius, the interaction approached significance ($F=1.44$, $p=0.06$, MSE $=0.048$).

4. Discussion

Our study investigated whether recall and recognition can be dissociated based on encoding-related brain activity. We found significant brain activations in both recognition > recall and recall > recognition contrasts. Because our design controlled for familiarity-based recognition, our findings necessarily reflect differential encoding processes supporting subsequent recollective-based recognition (untainted by familiarity) and subsequent-recall. Our results extend a previous study conducted in our lab which has shown that the recollective processes underlying recognition and recall can be dissociated based on retrieval-related MTL activity (Sadeh et al., 2011).

Critically, whereas previous studies which compared recognition and recall (Brassen et al., 2006; Habib & Nyberg, 2008; Staresina & Davachi, 2006) have shed light on brain mechanisms that show greater SM effects for recall than for recognition, our study is the first to examine the reverse contrast of recognition > recall. Our findings, therefore, provide novel evidence for the existence of encoding mechanisms that show greater SM effects for recognition than for recall.

Specifically, we found that the PHc and the posterior hippocampus are preferentially engaged in encoding activity predictive of subsequent recognition, as compared to subsequent recall. Because these regions have often been associated with processing of stimuli's contexts (Bar, Aminoff, & Schacter, 2008; Davachi, Mitchell, & Wagner, 2003; Davachi, 2006; Diana, Reder, Arndt, & Park, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Kahn, Davachi, & Wagner, 2004; Peters, Daum, Gizewski, Forsting, & Suchan, 2009; Prince, Daselaar, & Cabeza, 2005; Ranganath et al., 2003; Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001; Yonelinas, Otten, Shaw, & Rugg, 2005), our results suggest that recognition relies more on encoding-related contextual processing than does recall.

Why would encoding of context be more important in supporting successful subsequent recognition than successful subsequent recall? An influential cognitive model of memory provides a clue to this intriguing finding (Dennis & Humphreys, 2001). This model views recognition as a ''context-noise'' process, which requires participants to search for the specific context in which the physically presented test-item was studied, and distinguish between this ''studied context'' and other – task irrelevant – contexts. In contrast, recall is described to be an ''item-noise'' process. Here, participants must use contextual information to actively search for the target item and differentiate it from other items.

Though speculative, we wish to suggest that the ideas raised by this model may be in line with the role of context – and specifically, temporal context[3] – in our particular recall and recognition tests. In successful recall, the physical presentation of the cue word likely triggers the relevant temporal

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[3] Temporal context has been shown to underlie performance in memory tasks, including those applied in the current study (Polyn, Norman, & Kahana, 2009), and is of particular importance in elucidating retrieval patterns of individual, constantly-changing words in the list, which are embedded within the same external context.

context—namely, the temporal context which is identical, or very similar, to that of its target. This context triggers the search process for the relevant item. Therefore, recall requires an active search of the target-item, while the relevant temporal context is provided by a particularly effective cue—i.e., the cue word. In contrast, in recognition trials, each of the target and the three foils likely triggers its own, distinct, temporal context. Therefore, the temporal context needs to be encoded in finer resolution (as compared to recall) in order for participants to differentiate between the correct context – namely, that in which the cue appeared – and the incorrect contexts – namely, those elicited by the foils. Therefore, because recognition – but not recall – entails the identification of the studied context among irrelevant contexts, recognition is more dependent than recall on encoding temporal context at a finer resolution (for a similar idea regarding PHc activation during encoding, phrased in terms of interference rather than contextual processing see Kuhl, Shah, DuBrow, & Wagner, 2010). In line with these ideas regarding the role of temporal context in our study, two recent studies have shown that the PHc is specifically involved in processing temporal context (Jenkins & Ranganath, 2010; Tubridy & Davachi, 2010).

The differential roles of context in recall and recognition are also in line with results of a recent report from our lab, which used the exact same behavioral paradigm, but looked at retrieval (Sadeh et al., 2011). In that study, we showed that the retrieval process in recall is initiated by context-related PHc activity, which triggers activity in the hippocampus, presumably associated with reinstatement of the study episode. This hippocampal activity triggers activity in the Perirhinal cortex (PRc), a region associated with mnemonic processing of item information (Davachi, 2006; Diana et al., 2007). Interestingly, the reverse path was found for recognition—wherein retrieval was initiated by processing item information in the PRc and completed in retrieval of the relevant context by the PHc. Our current finding extends these previous results by showing that, while contextual processing plays a significant role in both recognition and recall during retrieval, processing contextual information during encoding is more crucial to differentiate between target and foils at recognition, than to initiate the retrieval process at recall. This finding provides an important constraint for theoretical models of memory.

Because processing of item information, as opposed to context information, is key in promoting recall, one might have expected the PRc to show an increase in activation during encoding supporting recall as compared to encoding supporting recognition. Our failure to find activity in the PRc in this contrast suggests that the PRc may play a somewhat different role in encoding as compared to retrieval. Whether this suggestion has merit remains to be investigated in future research.

Still, the notion that in recall encoding of item information is of particular importance may be in line with our finding of left iPFC activation in the recall > recognition contrast. This region has been suggested to play a role in the encoding of item information by selecting the relevant semantic features of the to-be-remembered items (Blumenfeld & Ranganath, 2007; Staresina & Davachi, 2006). Furthermore, as mentioned earlier, this region has been reported in previous investigations of encoding supportive of recall versus encoding supportive of recognition (Brassen et al., 2006; Staresina & Davachi, 2006).

Contrary to our findings, previous investigations of the contrast of recall > recognition also found hippocampal activation (Brassen et al., 2006; Habib & Nyberg, 2008; Staresina & Davachi, 2006). However, in those studies the same set of words was submitted to both recall and recognition and words that were both recalled and recognized were classified as recalled. Therefore, as compared to recognition, the set of words classified as recalled likely benefitted from additional relational encoding, which elicited enhanced hippocampal activity. In our task, however, each pair of words was submitted either to recall or to recognition, but never to both. Thus, words classified as recognized could have potentially been recalled. There is, therefore, no reason to assume that they benefitted less from hippocampal-based relational encoding.

Our finding of PHc and posterior hippocampus activity in the recognition > recall contrast contributes to a lively debate regarding the functional roles of distinct MTL sub-regions in memory operations. A common view is that each of the MTL sub-regions plays a different mnemonic function (Davachi et al., 2003, 2006; Davachi, 2006; Eichenbaum et al., 2007; Eldridge et al., 2000; Kahn et al., 2004; Peters et al., 2009; Prince et al., 2005; Ranganath et al., 2003; Yonelinas et al., 2001, 2005). In particular, this view argues for a specific role of the PHc and posterior hippocampus in mnemonic processing of contextual information. However, others have argued against this view, claiming that the functional distinctions between the MTL sub-regions are not well-supported by the current neuroscientific literature (e.g., Wixted & Squire, 2011). Our study provides evidence for a distinct role of the PHc and posterior hippocampus in encoding supporting recognition, which is most likely explained in terms of higher reliance on contextual processing (see above for discussion regarding recognition as a context-noise process). This result thus speaks in favor of the former view which argues for distinct functions of MTL sub-regions, and specifically in favor of the role of the PHc and posterior hippocampus in contextual processing.

A possible concern regarding our analyses arises from the potential confounding effects of presentation order, with words submitted to recognition presented before words submitted to recall. Additionally, words submitted to the recognition test were presented after a longer interval between study and test phases. One could argue that brain activity detected in the recognition > recall contrast was a result of the recognition effects being more robust than the recall effects because of more mental effort (or less fatigue) during encoding of words submitted to recognition, or by differences in noise levels between the two tests (caused, for instance, by scanner drift between the scans). However, this concern was alleviated by the inclusion of session regressors in our design, which captured the average brain activity in a session (see results for further details). These regressors partialled out differences which are attributed merely to the fact the recall and recognition trials were presented in different scans.

In addition to presentation order and the longer study-test interval before recognition, possible confounding differences in robustness may also be attributed to the different number of items presented in each test, with recall including more items than recognition. However, our findings of regions showing a greater SM effect in one test than in the other – as revealed by the interaction analysis we conducted – are not likely interpreted by differences in robustness between recall and recognition (due to any one of the reasons enumerated above). Thus, had our findings been only a function of robustness, similar activation would have been expected in both ’remembered’ and ’forgotten’ conditions within the same session and memory test, thereby canceling out the findings of differential SM effects. Therefore, specific differences in mnemonic operations at encoding, rather than general differences in robustness or mental effort, are most likely to account for our findings.

Most importantly – regarding possible confounding effects in robustness – we stress that the systematic differences we implemented between recall and recognition were necessary to control for the inherent confound of difficulty between the two tests, with recall generally being harder than recognition. Differences between the difficulty of recall and recognition tests are often interpreted in terms of differences in memory strength (e.g., Haist et al., 1992) and so may reflect specific mnemonic differences between the two tests. Therefore, it is vital to control for differences in difficulty, even at the expense of introducing systematic differences into the design—as we have intentionally done. This is because the differences we introduced likely do not reflect specific mnemonic differences, whereas differences in difficulty likely do.

In summary, our results reveal unique brain regions which are associated with encoding supporting recognition which are distinct from those associated with encoding supporting recall. These results provide novel evidence for dissociative encoding mechanisms supporting recollection-based recognition and recall, thus arguing against the widespread assumption that recollection-based recognition is a recall-like process.

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Appendix A. Supplementary information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2012.05.035.

References

Bar, M., Aminoff, E., & Schacter, D. L. (2008). Scenes unseen: the Parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *Journal of Neuroscience*, *28*, 8539–8544.

Blumenfeld, R. S., & Ranganath, C. (2007). Prefrontal cortex and long-term memory encoding: an integrative review of findings from neuropsychology and neuroimaging. *The Neuroscientist*, *13*, 280–291.

Brassen, S., Weber-Fahr, W., Sommer, T., Lehmbeck, J. T., & Braus, D. F. (2006). Hippocampal-prefrontal encoding activation predicts whether words can be successfully recalled or only recognized. *Behavioural Brain Research*, *171*, 271–278.

Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Making memories: brain activity that predicts how well visual experience will be remembered. *Science*, *281*, 1185–1187.

Cabeza, R., Kapur, S., Craik, F. I. M., McIntosh, A. R., Houle, S., & Tulving, E. (1997). Functional neuroanatomy of recall and recognition: a PET study of episodic memory. *Journal of Cognitive Neuroscience*, *9*, 254–265.

Cocosco, C. A., Kollokian, V., Kwan, R. K.-S., & Evans, A. C. (1997). BrainWeb: online interface to a 3DMRI simulated. *NeuroImage*, *5*, S425.

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*, 109–114.

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 2157–2162.

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*, 693.

Davelaar, E. J., Goshen-Gottstein, Y., Ashkenazi, A., Haarmann, H. J., & Usher, M. (2005). The demise of short-term memory revisited: empirical and computational investigations of recency effects. *Psychological Review*, *112*, 3–42.

Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(4), 791–808.

Dennis, S., & Humphreys, M. (2001). A context noise model of episodic word recognition. *Psychological Review*, *108*, 452–478.

Diana, R., Reder, L., Arndt, J., & Park, H. (2006). Models of recognition: a review of arguments in favor of a dual-process account. *Psychonomic Bulletin & Review*, *13*, 1–21.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends in Cognitive Sciences*, *11*, 379–386.

Dunn, J. C. (2008). The dimensionality of the remember-know task: a state-trace analysis. *Psychological Review*, *115*(2), 426–446.

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152.

Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neuroscience*, *3*, 1149–1152.

Guderian, S., Brigham, D., & Mishkin, M. (2011). Two processes support visual recognition memory in rhesus monkeys. *Proceedings of the National Academy of Sciences*, *108*(48), 19425–19430.

Habib, R., & Nyberg, L. (2008). Neural correlates of availability and accessibility in memory. *Cerebral Cortex*, *18*, 1720–1726.

Haist, F., Shimamura, A. P., & Squire, L. R. (1992). On the relationship between recall and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*, 691–702.

Haskins, A. L., Yonelinas, A. P., Quamme, J. R., & Ranganath, C. (2008). Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron*, *59*, 554–560.

Hirst, W., Johnson, M. K., Phelps, E. A., & Volpe, B. T. (1988). More on recognition and recall in amnesics. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *14*, 758–762.

Humphreys, M. S., Maguire, A. M., McFarlane, K. A., Burt, J. S., Bolland, S. W., & Murray, K. L. (2010). Using maintenance rehearsal to explore recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(1), 147–159.

Jenkins, L. J., & Ranganath, C. (2010). Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. *Journal of Neuroscience*, *30*, 15558–15565.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. *Journal of Neuroscience*, *24*, 4172–4180.

Kuhl, B. A., Shah, A. T., DuBrow, S., & Wagner, A. D. (2010). Resistance to forgetting associated with hippocampus-mediated reactivation during new learning. *Nature Neuroscience*, *13*, 501–506.

McDaniel, M. A., Einstein, G. O., DeLosh, E. L., May, C. P., & Brady, P. (1995). The bizarreness effect: it's not surprising, it's complex. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 422–435.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, *6*, 93.

Peters, J., Daum, I., Gizewski, E., Forsting, M., & Suchan, B. (2009). Associations evoked during memory encoding recruit the context-network. *Hippocampus*, *19*, 141–151.

Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review*, *116*, 129.

Prince, S. E., Daselaar, S. M., & Cabeza, R. (2005). Neural correlates of relational memory: successful encoding and retrieval of semantic and perceptual associations. *The Journal of Neuroscience*, *25*, 1203–1210.

Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M., & D'Esposito, M. (2003). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*, *42*, 2–13.

Rotello, C., & Heit, E. (2000). Associative recognition: a case of recall-to-reject processing. *Memory and Cognition*, *28*, 907–922.

Sadeh, T., Maril, A., Bitan, T., & Goshen-Gottstein, Y. (2011). Putting humpty together and pulling him apart: accessing and unbinding the hippocampal item-context engram. *NeuroImage*, *60*, 808–817.

Sanquist, T., Rohrbaugh, J., Syndulko, K., & Lindsley, D. (1980). Electrophysiological signs of levels of processing: perceptual analysis and recognition memory. *Psychophysiology*, *17*, 568–576.

Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: meta-analyses using activation likelihood estimation. *Neuropsychologia*, *47*, 1765–1779.

Staresina, B. P., & Davachi, L. (2006). Differential encoding mechanisms for subsequent associative recognition and free recall. *Journal of Neuroscience*, *26*, 9162–9172.

Stark, C. E. L., & Squire, L. R. (2001). When zero is not zero: the problem of ambiguous baseline conditions in fMRI. *Proceedings of the National Academy of Sciences*, *98*, 12760–12766.

Tubridy, S., & Davachi, L. (2010). Medial temporal lobe contributions to episodic sequence encoding. Cerebral Cortex.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*, 273–289.

Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., Rosen, B. R., & Buckner, R. L. (1998). Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*, 1188–1191.

Whittlesea, B. W. A., & Leboe, J. P. (2000). The heuristic basis of remembering and classification: fluency, generation, and resemblance. *Journal of Experimental Psychology: General*, *129*, 84.

Wixted, J. T., & Squire, L. R. (2011). The medial temporal lobe and the attributes of memory. *Trends in Cognitive Sciences*, *15*, 210–217.

Yonelinas, A. P. (1997). Recognition memory ROCs for item and associative information: evidence for a dual-process signal-detection model. *Memory and Cognition*, *25*, 747–763.

Yonelinas, A. P., Hopfinger, J. B., Buonocore, M. H., Kroll, N. E. A., & Baynes, K. (2001). Hippocampal, Parahippocampal and occipital-temporal contributions to associative and item recognition memory: an fMRI study. *NeuroReport*, *12*, 359–363.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: a review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.

Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *The Journal of Neuroscience*, *25*, 3002–3008.