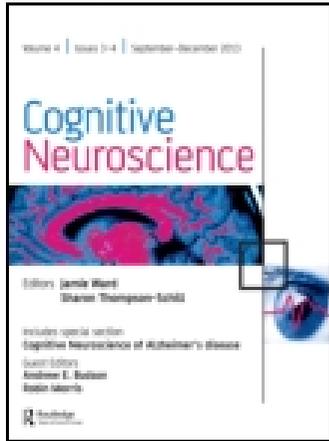


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### False memory for context activates the parahippocampal cortex

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## Report

# False memory for context activates the parahippocampal cortex

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Previous studies have reported greater activity in the parahippocampal cortex during true memory than false memory, which has been interpreted as reflecting greater sensory processing during true memory. However, in these studies, sensory detail and contextual information were confounded. In the present fMRI study, we employed a novel paradigm to dissociate these factors. During encoding, abstract shapes were presented in one of two contexts (i.e., moving or stationary). During retrieval, participants classified shapes as previously “moving” or “stationary.” Critically, contextual processing was relatively greater during false memory (“moving” responses to stationary items), while sensory processing was relatively greater during true memory (“moving” responses to moving items). Within the medial temporal lobe, false memory versus true memory produced greater activity in the parahippocampal cortex, whereas true memory versus false memory produced greater activity in the hippocampus. The present results indicate that the parahippocampal cortex mediates contextual processing rather than sensory processing.

**Keywords:** True memory; Illusory memory; Source memory; Hippocampus; fMRI.

Medial temporal lobe subregions play integral roles during true memory and false memory. Cabeza, Rao, Wagner, Mayer, and Schacter (2001) were the first to assess whether activity in medial temporal lobe subregions distinguished between true memory and false memory. They implemented a modified version of the Deese-Roediger-McDermott paradigm (Deese, 1959; Roediger & McDermott, 1995). At study, participants watched video clips of speakers reading categorized word lists (e.g., water, freeze, wet, etc.) that were each related to a critical nonpresented word (e.g., cold). At test, participants were presented with old items, related items, and new items during functional magnetic resonance imaging (fMRI). True memory (i.e., old item hits) produced greater activity than false memory (i.e., related item false alarms) in the parahippocampal cortex. Cabeza et al. (2001)

postulated that this parahippocampal cortex activity reflected recovery of sensory information, as true memories have greater sensory detail than false memories (Mather, Henkel, & Johnson, 1997; Norman & Schacter, 1997). Subsequent studies that employed categorized picture lists (Gutchess & Schacter, 2012) and picture perception or imagery (Okado & Stark, 2003) also reported greater parahippocampal cortex activity during true memory than false memory, and a recent study that used pairs of pictures with the same verbal label observed greater parahippocampal cortex activity during true recollection than false recollection (Abe et al., 2013). To our knowledge, the opposite comparison—false memory versus true memory—has never produced activity in the parahippocampal cortex (but see, Dennis, Bowman, & Vandekar, 2012; Stark, Okado, & Loftus, 2010).

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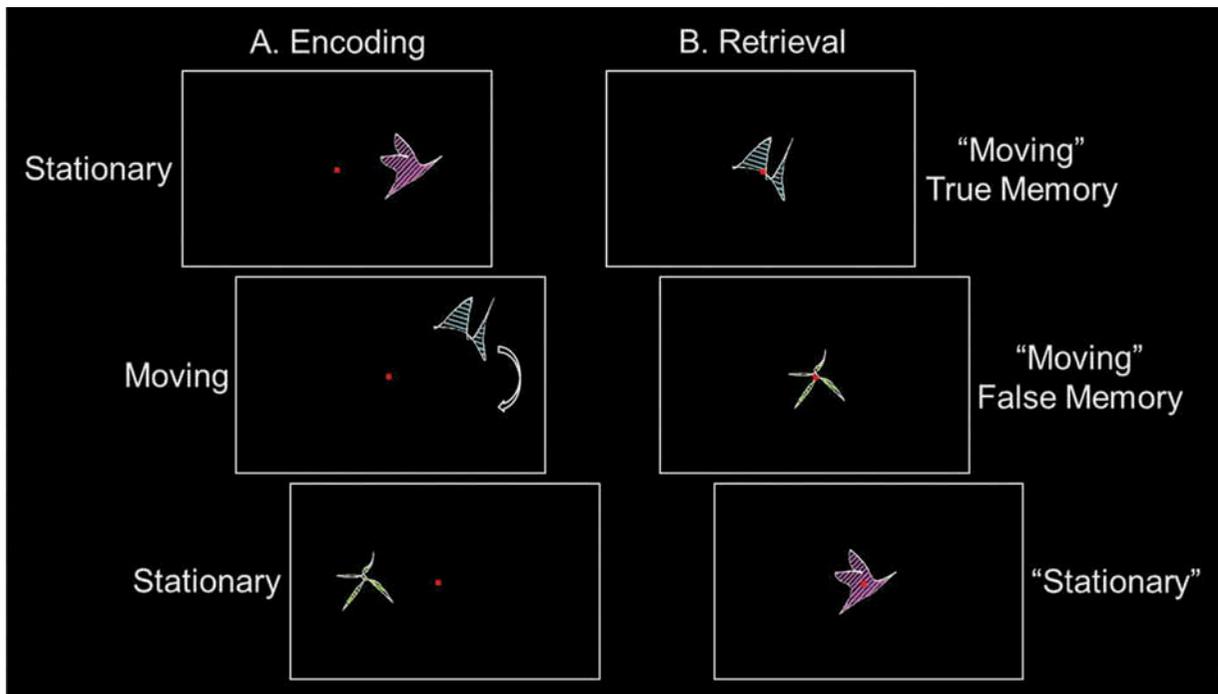
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The preceding evidence suggests that activity in the parahippocampal cortex may always be greater during true memory than false memory. As mentioned previously, this may be because true memories are associated with greater sensory detail, which is consistent with the hypothesis that the parahippocampal cortex mediates visual spatial processing, such as visual size or spatial layout (Epstein & Kanwisher, 1998; Epstein & Ward, 2010; Troiani, Stigliani, Smith, & Epstein, 2014; note that all of the protocols described above involved pictorial stimuli). Alternatively, it has been hypothesized that the parahippocampal cortex mediates contextual processing, such as the source of previously presented items (Eichenbaum, Sauvage, Fortin, Komorowski, & Lipton, 2012; Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Slotnick, 2013). Critically, both sensory detail and contextual information were greater during true memory than false memory in the above-mentioned memory studies (i.e., these factors were confounded). Therefore, the role of the parahippocampal cortex during true memory and false memory is uncertain.

In the present study, we aimed to dissociate sensory processing and contextual processing such that false memories would require greater contextual processing than true memories. During encoding, abstract shapes were presented in either one of two contexts (i.e., moving or stationary; Figure 1A). During retrieval, old

items from encoding were presented at fixation and participants identified the previous context of each item (i.e., “moving” or “stationary”; Figure 1B). True memory corresponded to a “moving” response to a previously moving item. False memory corresponded to a “moving” response to a previously stationary item (i.e., the incorrect generation of context), which is similar to the incorrect generation of a critical nonpresented word during the Deese-Roediger-McDermott paradigm (as opposed to a “stationary” response to a previously moving item, which is more aptly described as forgetting the feature of motion).

Of importance, item information and contextual information are sometimes integrated, particularly when the contextual information can be considered an item feature (cf., Diana, Yonelinas, & Ranganath, 2010; Staresina & Davachi, 2008). As such, true memories in the present paradigm can be assumed to be based on such integrated trials, which do not involve separate contextual processing, and other trials in which item and contextual information are processed separately. By contrast, all false memories reflect incorrect contextual assignment (i.e., incorrectly assigning a stationary item to the “moving” context/source). Thus, across all trials in the present paradigm, it can be assumed that false memories require a greater degree of contextual processing than true memories. If the parahippocampal cortex mediates sensory processing



**Figure 1.** Stimulus protocol. (A) During encoding, moving and stationary shapes were presented to the left or right of fixation. (B) During retrieval, shapes were presented at fixation and participants classified each item as previously “moving” or “stationary.”

(Epstein & Kanwisher, 1998; Epstein & Ward, 2010; Troiani et al., 2014), then activity in this region will be greater for true memories than false memories, as true memories are associated with greater sensory detail. Alternatively, if the parahippocampal cortex mediates contextual processing (Eichenbaum et al., 2007, 2012; Ranganath, 2010; Slotnick, 2013), then activity in this region will be greater for false memories than true memories. That is, in the present paradigm, these hypotheses predict the opposite pattern of activity in the parahippocampal cortex.

## METHOD

Twelve Boston College students completed the study (nine females, age range 19–28 years). Participants were right-handed native English speakers with normal or corrected-to-normal vision. Each participant was compensated \$10 for the behavioral training session and \$25 per hour for fMRI. The Boston College Institutional Review Board approved the behavioral protocol and the Massachusetts General Hospital Institutional Review Board approved the fMRI protocol. Informed and written consent was obtained before each session.

Each participant completed a one-quarter length run and two full-length runs during the behavioral training session and six full-length runs during fMRI. They were instructed to always maintain fixation and remember whether each shape was moving or stationary and its spatial location. During the encoding phase of each full-length run, 24 abstract shapes were presented in the left or right visual field along an arc spanning  $\pm 45^\circ$  of polar angle from the horizontal meridian. Each shape spanned  $4^\circ$  of visual angle with the nearest edge  $2^\circ$  of visual angle from fixation. The shapes were designed to minimize verbal encoding strategies (for details on shape construction, see, Slotnick & Schacter, 2004). Each shape was presented for 2.5 seconds with an inter-trial-interval of 3.0 seconds. Shape sets were repeated three times during encoding with each shape set randomized and presented sequentially. An equal number of shapes were stationary, at one of six equally spaced locations along the stimulation arc within each hemifield, or moving, smoothly traversing the entire stimulation arc in each hemifield with either upward or downward motion. In each run, all spatial locations and movement directions were presented equally often. Before the retrieval phase, an instruction screen was presented for 8.0 seconds that reminded participants to maintain fixation and displayed the response mappings. During each retrieval phase, the shapes from encoding were

presented in random order at fixation for 3.5 seconds with an inter-trial-interval of 7–10 seconds. Participants pressed a response button with the fingers of their left hand to classify each shape as “previously moving in the left visual field,” “previously moving in the right visual field,” “previously stationary in the left visual field,” or “previously stationary in the right visual field.” Participants also made a subsequent “remember”-“know” response to characterize their subjective experience. During encoding and retrieval, no more than three shapes of a given type were presented sequentially. Shapes were never repeated across runs. Sets of shapes (moving-left, moving-right, stationary-left, and stationary-right) were counterbalanced across participants using a Latin Square design.

Imaging data were acquired on a Siemens 3 Tesla Trio Scanner with a standard head coil (Erlangen, Germany). Functional images were acquired with an echo planar imaging sequence (TR = 2000 ms, TE = 20 ms, flip angle =  $90^\circ$ , field-of-view =  $256 \times 256 \text{ mm}^2$ , acquisition matrix =  $64 \times 64$ , slices = 33, slice thickness = 4 mm, 4 mm isotropic resolution). Anatomic images were acquired with a magnetized prepared rapid gradient echo sequence (TR = 30 ms, TE = 3.3 ms, flip angle =  $40^\circ$ , field-of-view =  $256 \times 256 \text{ mm}^2$ , acquisition matrix =  $256 \times 256$ , slices = 128, slice thickness = 1.33 mm,  $1.33 \times 1 \times 1 \text{ mm}$  resolution). Analyses were conducted using Brain Voyager QX. Voxels were resampled at  $3 \text{ mm}^3$ . Pre-processing included slice-time correction, motion correction, and temporal filtering by removal of linear trends and components at or below 2 cycles per run length (using a general linear model to remove low frequency Fourier basis sets). To maximize spatial resolution, spatial smoothing was not conducted. Functional and anatomic images were transformed into Talairach space.

To maximize power, unless stated otherwise, we collapsed over spatial location and remember-know responses. Activations were localized on the group average anatomic volume. For all contrasts, an individual voxel threshold of  $p < .001$  was enforced, false discovery rate corrected for multiple comparisons to  $p < .05$ . It should be mentioned that this method of correction for multiple comparisons limits the number of false positives but does not require a minimum spatial extent (Logan & Rowe, 2004). Only activations in the medial temporal lobe—the parahippocampal cortex, the hippocampus, the entorhinal cortex, and the perirhinal cortex—were reported (other cortical activations are detailed in a separate manuscript; Karanian & Slotnick, 2014). Activations were localized based on the known anatomical distinctions of the medial temporal lobe

(Bernasconi et al., 2003; Insausti et al., 1998; Malykhin et al., 2007; Pruessner et al., 2000, 2002).

## RESULTS

Behavioral accuracy for classifying moving items and stationary items was at an intermediate level ( $69.1 \pm 3.0\%$  correct; mean  $\pm$  1 standard error). The contrast of false memory versus true memory for motion (“moving”/stationary items > “moving”/moving items) only produced activity in the parahippocampal cortex (Figure 2A; Table 1, top). The contrast of true memory versus false memory for motion (“moving”/moving items > “moving”/stationary items) only produced activity in the hippocampus (Figure 2B; Table 1, bottom). None of

**TABLE 1**  
Medial temporal lobe activations

Region	x	y	z	size (mm <sup>3</sup> )
<i>False memory &gt; true memory</i>				
Parahippocampal cortex	26	-26	-16	54
Parahippocampal cortex	22	-29	-15	27
Parahippocampal cortex	-19	-32	-9	27
Parahippocampal cortex	23	-41	-6	27
Parahippocampal cortex	25	-52	-3	54
<i>True memory &gt; false memory</i>				
Hippocampus	23	-6	-21	27
Hippocampus	17	-30	0	27
Hippocampus	14	-32	0	54

*Note:* Talairach coordinates (x, y, z) refer to the center of each activation.

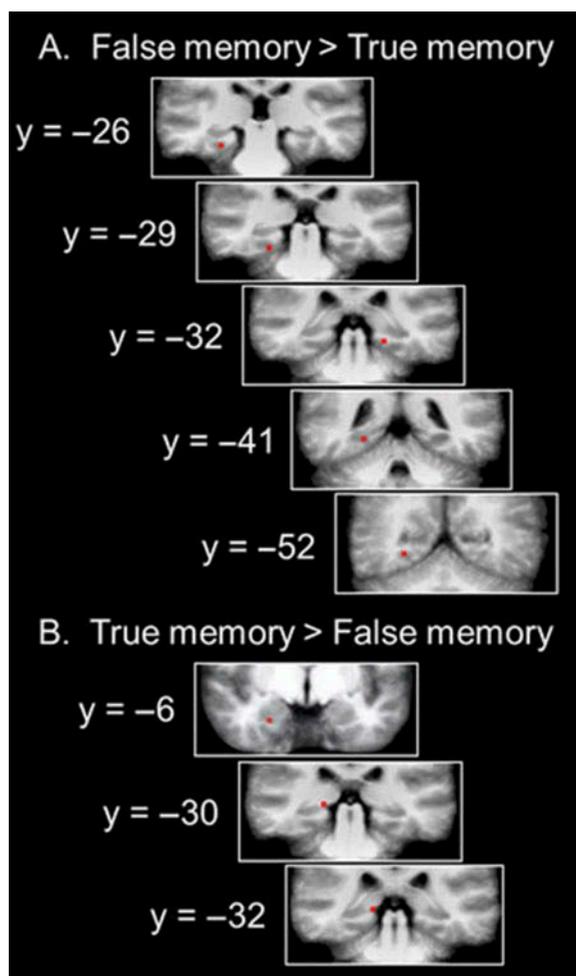
the activations spanned more than one subregion of the medial temporal lobe.

Previous evidence indicates that the parahippocampal cortex is associated with recollection to a greater degree than familiarity (for a review, see, Slotnick, 2013). As such, it is possible that the parahippocampal activity during false memory reflected recollection rather than contextual processing. However, “remember” rates were significantly greater for true memories than false memories ( $t(11) = 2.35, p < .05$ ), which rules out the possibility that there was a greater degree of recollection during false memory than true memory and indicates that activity in this region reflected contextual processing.

An additional analysis was conducted to assess whether the present pattern of activity stemmed from differences in confidence/remember rates between true memory and false memory. To address this possibility, the contrast of false memory versus true memory for motion was conducted with only “remember” responses, which produced the identical pattern of activity described above. Therefore, the present pattern of results was not due to confidence differences between true memory and false memory.

## GENERAL DISCUSSION

Of direct relevance to the hypotheses of interest, we found that false memory versus true memory only produced activity in the parahippocampal cortex. This is the first time, to our knowledge, that false memory has produced greater activity than true memory in the parahippocampal cortex, as previous studies have only reported the opposite finding of greater true memory/recollection than false memory/recollection activity in this region (Abe et al., 2013; Cabeza et al., 2001; Gutchess & Schacter, 2012; Okado & Stark, 2003). The present results support



**Figure 2.** Medial temporal lobe activations. (A) False memory > true memory activations. (B) True memory > false memory activations. Each activation is shown in red on a coronal slice at the specified y-coordinate (the left hemisphere is on the right).

the hypothesis that the parahippocampal cortex mediates contextual processing, which was greater for false memories than true memories in the present paradigm, rather than sensory processing, which was greater for true memories than false memories.

In the current study, false memories can be described from a source memory perspective. During encoding, items were presented in one of two contexts (i.e., moving or stationary). During retrieval, some previously stationary items were associated with little or no contextual information (e.g., due to lack of attention at encoding), and participants selected one of the two contexts/sources. Thus, in the present paradigm, an incorrect source response of “moving” to a previous stationary item was equivalent to a false memory for the context of motion. Along these lines, we contrasted incorrect spatial location/source responses (“right”/left items and “left”/right items) with correct spatial location/source responses (“right”/right items and “left”/left items), which only produced activity in the parahippocampal cortex. In a recent study (Abe et al., 2013), pictures were presented during encoding. During retrieval, same, similar, and new pictures were presented and participants made remember-know-new judgments. Familiarity-based false memories (i.e., “know same” responses to similar items) produced greater activity in the parahippocampal cortex than familiarity-based true memories (i.e., “know same” responses to same items). In this case, for weakly encoded items, participants may have selected the source (i.e., same or similar), where an incorrect source response of “know same” to a similar item can be described as a false memory. Therefore, in both the present study and this recent study (Abe et al., 2013), it appears that more weakly encoded items yielded greater reliance on source processing—and produced greater activity in the parahippocampal cortex—during familiarity-based false memories than during familiarity-based true memories (see also, Kim & Cabeza, 2007). Future work will be needed to assess whether such familiarity-based false memories consistently activate the parahippocampal cortex to a greater degree than familiarity-based true memories.

More broadly, the parahippocampal cortex has been hypothesized to mediate either visual spatial processing (Epstein & Kanwisher, 1998; Epstein & Ward, 2010; Troiani et al., 2014) or contextual processing (Eichenbaum et al., 2007, 2012; Ranganath, 2010; Slotnick, 2013). Epstein and Ward (2010) argued that parahippocampal activation during source memory tasks may reflect spatial aspects of the encoding episode. A behavioral analysis was conducted to

assess whether or not the activity observed in the parahippocampal cortex was driven by greater spatial processing for false memories than true memories. This analysis revealed that spatial location accuracy (i.e., memory for which side of the screen an item was previously presented) for true memory was significantly greater than spatial location accuracy for false memory ( $t(11) = 2.77, p < .05$ ). Moreover, the false memory versus true memory fMRI contrast was conducted with spatial location accuracy constant (i.e., incorrect), and the identical pattern of results was obtained. Thus, in the present paradigm, false memory-related parahippocampal activity appears to depend on contextual processing rather than spatial processing. Our findings are consistent with previous studies that reported parahippocampal activation during source memory for color (Diana et al., 2010; Ranganath et al., 2004) or task (word reading or imagery, Davachi, Mitchell, & Wagner, 2003; whether an item was animate or common, Kensinger & Schacter, 2006a), which do not involve spatial processing.

As mentioned previously, we assumed that a substantial proportion of true memories were based on the integration of item information and contextual information. This seems plausible as contextual information—whether a shape was moving or stationary—can be considered an item feature (see, Staresina & Davachi, 2008). By comparison, during false memories, item information and contextual information were never integrated because contextual assignment was incorrect. As a greater proportion of true memories than false memories can be assumed to be integrated, it follows that false memories required a relatively greater degree of contextual processing. Still, the assumption that true memories were based on relatively greater integration of item information and contextual information is a limitation of the present study that warrants further investigation.

We also found hippocampal activation was greater during true memory than false memory. Previous studies have also reported greater true memory than false memory activity in the hippocampus (Giovanello, Kensinger, Wong, & Schacter, 2010; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). However, the majority of studies that have compared true memory and false memory have not observed differential activity in the hippocampus (Cabeza et al., 2001; Kensinger & Schacter, 2006b; Slotnick & Schacter, 2004; Stark et al., 2010). Furthermore, most studies have reported hippocampal activity during both true memory (Cabeza et al., 2001; Dennis et al., 2012; Gutchess & Schacter, 2012; Kensinger & Schacter, 2006b; Kim

& Cabeza, 2007; Paz-Alonso et al., 2008; Slotnick & Schacter, 2004) and false memory (Cabeza et al., 2001; Dennis et al., 2012; Gutchess & Schacter, 2012; Slotnick & Schacter, 2004; Stark et al., 2010). Considered together, these results suggest that there may be somewhat greater hippocampal activation during true memories than false memories under certain conditions, but the hippocampus appears to be a critical region during the construction of both true memories and false memories (Schacter, Norman, & Koutstaal, 1998).

Of direct relevance to our aim, we dissociated sensory processing from contextual processing by employing a paradigm in which false memories reflected source memory. We found that parahippocampal activity tracked contextual processing during false memory rather than sensory processing during true memory. One limitation of the present study is that our paradigm involved memory for spatial location, thus our results are not completely immune from a visual spatial interpretation (see, Epstein & Ward, 2010). The present results would be bolstered by eliminating any spatial memory component from the paradigm, such as in a source memory for color task where all the stimuli are presented centrally. This is a topic of future research.

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