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False memory for context and true memory for context similarly activate the parahippocampal cortex

Jessica M. Karanian* and Scott D. Slotnick

Department of Psychology, Boston College, Chestnut Hill, MA, USA

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ABSTRACT

The role of the parahippocampal cortex is currently a topic of debate. One view posits that the parahippocampal cortex specifically processes spatial layouts and sensory details (i.e., the *visual-spatial processing view*). In contrast, the other view posits that the parahippocampal cortex more generally processes spatial and non-spatial contexts (i.e., the *general contextual processing view*). A large number of studies have found that true memories activate the parahippocampal cortex to a greater degree than false memories, which would appear to support the visual-spatial processing view as true memories are typically associated with greater visual-spatial detail than false memories. However, in previous studies, contextual details were also greater for true memories than false memories. Thus, such differential activity in the parahippocampal cortex may have reflected differences in contextual processing, which would challenge the visual-spatial processing view. In the present functional magnetic resonance imaging (fMRI) study, we employed a source memory paradigm to investigate the functional role of the parahippocampal cortex during true memory and false memory for contextual information to distinguish between the visual-spatial processing view and the general contextual processing view. During encoding, abstract shapes were presented to the left or right of fixation. During retrieval, old shapes were presented at fixation and participants indicated whether each shape was previously on the “left” or “right” followed by an “unsure”, “sure”, or “very sure” confidence rating. The conjunction of confident true memories for context and confident false memories for context produced activity in the parahippocampal cortex, which indicates that this region is associated with contextual processing. Furthermore, the direct contrast of true memory and false memory produced activity in the visual cortex but did not produce activity in the parahippocampal cortex. The present evidence suggests that the parahippocampal cortex is associated with general contextual processing rather than only being associated with visual-spatial processing.

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* Corresponding author. Boston College, Department of Psychology, McGuinn Hall, Room 316, 140 Commonwealth Avenue, Chestnut Hill, MA 02467, USA.

E-mail address: jessica.karanian@bc.edu (J.M. Karanian).

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1. Introduction

In a large number of studies within the field of perception, the parahippocampal cortex has been associated specifically with visual-spatial processing. For instance, the parahippocampal cortex has been shown to play a critical role in scene perception, navigation through space, and spatial representation (e.g., Aguirre, Detre, Alsop, & D'Esposito, 1996; Aguirre & D'Esposito, 1998; Epstein, 2008; Epstein & Kanwisher, 1998; Epstein & Ward, 2010; Epstein, Harris, Stanley, & Kanwisher, 1999; Janzen, Wagensveld, & van Turenout, 2007; Mullally & Maguire, 2011; Troiani, Stigliani, Smith, & Epstein, 2014). Such evidence has contributed to the view that the primary function of the parahippocampal cortex is to process visual-spatial information (i.e., the *visual-spatial processing view*; Epstein & Ward, 2010).

In contrast, within the field of memory, there is evidence that the parahippocampal cortex plays a critical role more broadly in contextual processing, as indicated by its involvement in recollection, associative memory, and source memory (e.g., Davachi, Mitchell, & Wagner, 2003; Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Ranganath et al., 2004; Slotnick, 2013a, 2013b; Tendolkar et al., 2008; Wang, Yonelinas, & Ranganath, 2013). For instance, in one study, activity in the parahippocampal cortex was correlated with the amount of contextual information retrieved (Tendolkar et al., 2008). Images were presented in varying shades of red or green during the encoding phase. During retrieval, old and new gray images were presented and participants made old-new recognition judgments and then provided two context memory judgments for old items. They identified whether images were previously red or green (i.e., context judgment 1) and identified the particular shade of red or green (i.e., context judgment 2). Analysis of retrieval-related activity in the parahippocampal cortex revealed a linear increase based on the amount of context information retrieved (i.e., item and no context < item and 1 context < item and 2 contexts). Such evidence provides strong support for the view that the parahippocampal cortex plays a critical role in the retrieval of contextual information. However, many memory studies have employed paradigms that involved some degree of visual-spatial processing. Such paradigms have included scene processing (e.g., Davachi et al., 2003; Duarte, Henson, & Graham, 2011; Kahn, Davachi, & Wagner, 2004), spatial location processing (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Ross & Slotnick, 2008), and item size judgments (e.g., Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011). As a result, proponents of the visual-spatial processing view have suggested that activity in the parahippocampal cortex observed during memory studies can be attributed to the inherent visual-spatial processing induced by the paradigms employed (see Epstein & Ward, 2010). However, other memory studies have shown that the parahippocampal cortex is associated with processing of non-spatial information (e.g., Diana, *in press*; Kirwan & Stark, 2004; Ranganath et al., 2004). For instance, Diana (*in press*) implemented a paradigm that was devoid of spatial processing. At encoding, participants were presented words and asked one of four different non-spatial questions related to each word (e.g., “is this a noun or verb?” or “is this word

common or uncommon?”). At retrieval, participants completed an old-new recognition task for each item (i.e., the word) and then identified its associated context (i.e., the question). Directly challenging the visual-spatial processing view, non-spatial memories for context were associated with activity in the parahippocampal cortex. Such non-spatial evidence supports the *general contextual processing view* of the parahippocampal cortex.

Of direct relevance to the present investigation, a number of false memory studies have reported that the magnitude of activity in the parahippocampal cortex is greater during true memories than false memories (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Dennis, Bowman, & Vandekar, 2012; Dennis, Johnson, & Peterson, 2014; Kahn et al., 2004; Giovanello, Kensinger, Wong, & Schacter, 2009; Kim & Cabeza, 2007; Kurkela & Dennis, 2016; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). As true memories are often associated with greater visual-spatial detail than false memories (Karanian & Slotnick, 2014a, 2017; Mather, Henkel, & Johnson, 1997; Norman & Schacter, 1997; Slotnick & Schacter, 2004), it is possible that differential activity observed in the parahippocampal cortex in previous studies (e.g., Cabeza et al., 2001; Kahn et al., 2004) reflected differences in visual-spatial processing during retrieval. However, in these false memory studies, contextual details were also greater for true memory than false memory; thus, the differential activity in the parahippocampal cortex could also have reflected greater contextual processing during true memories than false memories. Thus, it remains uncertain whether the true memory versus false memory differential activity in the parahippocampal cortex reflected differences in visual-spatial detail, which would provide support for the visual-spatial processing view, or differences in contextual processing, which would provide support for the general contextual processing view.

False memory studies have also employed source memory paradigms. In these paradigms, items are presented in a particular context/source during encoding (e.g., on a green background or on a red background), and then during retrieval participants identify the previous context (e.g., “green” or “red”) of each item. The parahippocampal cortex has been associated with both true memory for contextual information (e.g., Davachi et al., 2003; Kensinger & Schacter, 2006; Ranganath et al., 2004) and false memory for contextual information (Karanian & Slotnick, 2014b; Stark, Okado, & Loftus, 2010), where old items from encoding were attributed to the wrong context (i.e., source misattribution errors). For instance, one study employed a paradigm in which items were presented either visually or auditorily during encoding (Stark et al., 2010). During retrieval, old items were presented and participants identified whether each was previously presented within the visual or auditory modality. False memories for the visual context (i.e., “visual”/auditory) were associated with activity in the parahippocampal cortex. Similarly, in a recent study, we employed a paradigm in which items were presented as either moving or stationary during encoding (Karanian & Slotnick, 2014b). During retrieval, old items were presented and participants identified the context of each item as previously “moving” or “stationary”. False memories for the context of motion (i.e., “moving”/stationary) produced activity

in the parahippocampal cortex. The evidence from these studies suggests that false memory for context, like true memory for context, is associated with the parahippocampal cortex. Such evidence supports the general contextual processing view of the parahippocampal cortex. However, these studies are not immune from the visual-spatial processing account. For instance, it is conceivable that the visual context induced more visual-spatial processing than the auditory context (Stark et al., 2010) and that the motion context induced more visual-spatial processing than the stationary context (Karanian & Slotnick, 2014b). Thus, the role of the parahippocampal cortex during the construction of false memories for context remains uncertain.

In the present fMRI study, we employed a source memory paradigm to assess the role of the parahippocampal cortex during true memories for context and false memories for context to distinguish between the visual-spatial processing view and the general contextual processing view. Accordingly, we assessed the relative magnitude of activity in the parahippocampal cortex during true memories for context and false memories for context. Under the assumption that true memories for context are often associated with greater visual-spatial detail than false memories (Karanian & Slotnick, 2014a, 2017; Mather et al., 1997; Norman & Schacter, 1997; Slotnick & Schacter, 2004), the two views predict different patterns of parahippocampal activity. The visual-spatial processing view predicts that parahippocampal activity will be greater in magnitude during true memories for context than false memories for context because true memories are associated with greater visual-spatial processing than false memories. Alternatively, the general contextual processing view predicts that the magnitudes of parahippocampal activity will be similar during true memories for context and false memories for context because both types of memories are associated with similar degrees of contextual processing. We also expected to find that confident true memories and confident false memories for context would be associated with activity in other context processing regions including the hippocampus, the retrosplenial cortex, and the medial prefrontal cortex (e.g., Aminoff, Kveraga, & Bar, 2013; Bar, Aminoff, & Schacter, 2008; Ranganath, 2010; Rugg & Vilberg, 2013; Slotnick, 2010b). To anticipate the results, we found that true memories for context and false memories for context activated the parahippocampal cortex to a similar degree, which provides support for the general contextual processing view.

2. Material and methods

2.1. Participants

Sixteen students from Boston College (12 females, age range 20–29 years old) participated in the study. Participants were right-handed, native English speakers, and had normal or corrected-to-normal vision. The Boston College Institutional Review Board approved the protocols. Informed and written consent was obtained before each session. Participants were compensated \$10 for the behavioral training session and \$25/h for the fMRI session.

2.2. Stimuli and procedure

During fMRI, participants completed either 7 or 8 memory runs. Fourteen participants completed 8 memory runs, one participant completed 7 runs due to timing limitations, and one participant completed 7 runs due to a stimulus presentation programming error. For each run, during the encoding phase, 32 colored abstract shapes spanning 6.7° of visual angle were presented in the left or right visual field with the nearest edge 3.6° of visual angle from fixation (Fig. 1A; for shape construction details, see Slotnick & Schacter, 2004). Each shape was presented for 2.5 sec followed by a .5 sec fixation period. Shape sets were randomized and presented sequentially two times (each shape was presented at only one spatial location). Participants were instructed to remember each shape and its spatial location. Immediately after the encoding phase and before the retrieval phase, an instruction screen was displayed for 8.0 sec followed by a 2.0 sec fixation period. During the retrieval phase of each run, shapes from encoding were randomized and presented sequentially at fixation (Fig. 1B). New shapes were not presented during the retrieval phase. Each shape spanned 6.7° of visual angle and was presented for 3.0 sec (Fig. 1). Immediately after each shape, a confidence rating (U S V) screen was presented for 2.5 sec followed by a fixation period of .5–4.5 sec. This resulted in an inter-trial-interval of 6.0–10.0 sec, which is sufficient to allow for the deconvolution of the hemodynamic response. Participants classified each shape as previously in the “left” or “right” visual field and then made a confidence response (“unsure”, “sure”, “very sure”). If the participant did not make a spatial location response while the stimulus was presented and a confidence rating response while the confidence rating screen was presented, this was classified as a no-response trial. During both encoding and retrieval, no more than three items of a given type (i.e., left spatial location or right spatial location) were sequentially presented and participants were instructed to maintain fixation. Shapes were never repeated across runs. The spatial location of each shape (left, right) was counterbalanced across participants using a Latin Square design.

Confident true memories for context were defined as a correct spatial context response with a high or medium confidence rating (left-“left”-“very sure”, right-“right”-“very sure”, left-“left”-“sure”, or right-“right”-“sure”), while low confidence true memories for context were defined as a correct spatial context response with a low confidence rating (left-“left”-“unsure” or right-“right”-“unsure”). Confident false memories for context were defined as an incorrect spatial context response with a high or medium confidence rating (left-“right”-“very sure”, right-“left”-“very sure”, left-“right”-“sure”, or right-“left”-“sure”), while low confidence false memories for context were defined as an incorrect spatial context response with a low confidence rating (left-“right”-“unsure” or right-“left”-“unsure”).

2.3. Data acquisition and analysis

Data were acquired using a Siemens 3 Tesla Trio Scanner (Erlangen, Germany) with a 32-channel head coil. Functional images were acquired with an echo planar imaging sequence (TR = 2000 msec, TE = 30 msec, flip angle = 90°, field-of-

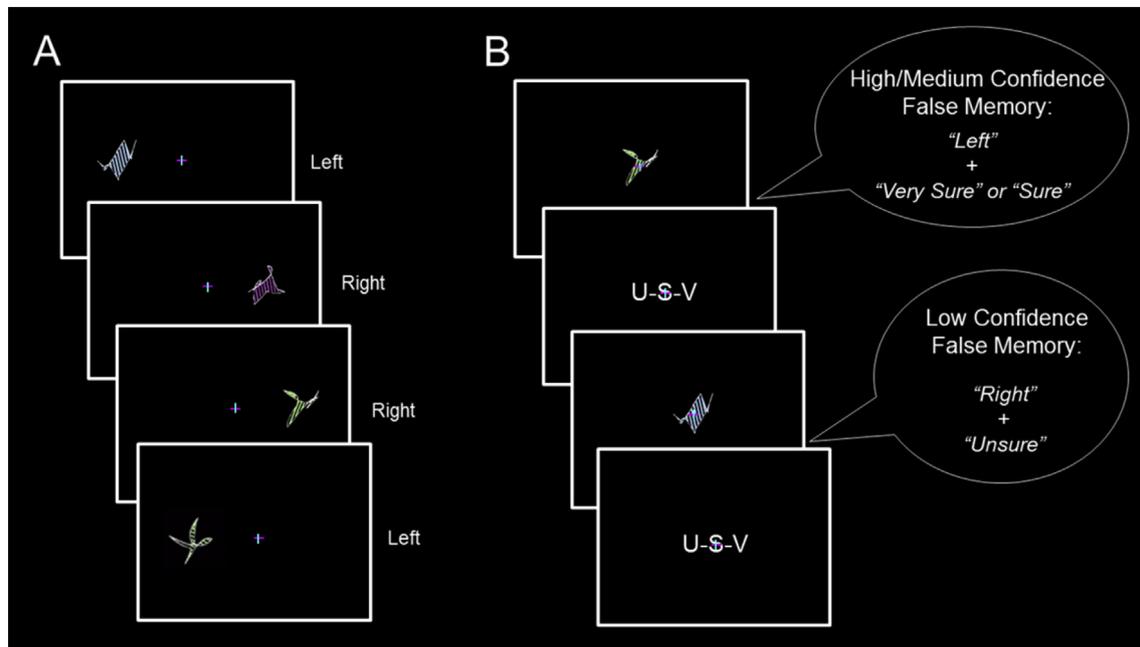


Fig. 1 – Context memory paradigm. A, During encoding, shapes were presented in the left visual field or the right visual field (item types are shown to the right). B, During retrieval, shapes were presented in the center of the screen and participants identified each as previously in the “left” or “right” visual field, followed by an “unsure”-“sure”-“very sure” confidence rating (illustrative responses are displayed to the right).

view = 256×256 mm, acquisition matrix = 64×64 , slices = 33, slice acquisition order = interleaved bottom-to-top, slice thickness = 4 mm, no gap; 4 mm isotropic resolution). Anatomic images were acquired with a magnetized prepared rapid gradient echo sequence (TR = 30 msec, TE = 3.3 msec, flip angle = 40° , field-of-view = 256×256 mm, acquisition matrix = 256×256 , slices = 128, slice thickness = 1 mm; $1.33 \times 1 \times 1$ mm resolution). Analyses were conducted with Brain Voyager QX (Brain Innovation B.V., Maastricht, The Netherlands). 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). Voxels were resampled at $3 \times 3 \times 3$ mm. To maximize spatial resolution, spatial smoothing was not conducted. Anatomic and functional images were transformed into Talairach space.

A random-effect general linear model was conducted. The protocol of each event (i.e., a square wave defined by each event onset and the subsequent behavioral response) was convolved with a canonical hemodynamic response function to produce each hemodynamic response model for every participant. Both encoding trials and no-response trials during retrieval (i.e., trials in which no response was provided) were assumed to have durations of 2.5 sec. The mean level of activity for each run was also modeled with a constant.

A whole-brain analysis was conducted. Only activations in our regions of interest were considered: the parahippocampal cortex, the hippocampus, the retrosplenial cortex, the medial prefrontal cortex, and visual processing regions. These regions were selected based on prior evidence that they play an important role in memory for visual associative/contextual information (e.g., Aminoff et al., 2013; Bar et al., 2008;

Ranganath, 2010; Rugg & Vilberg, 2013; Slotnick, 2010b). Other areas of activation are available upon request from J.M.K. Medial temporal lobe regions were localized on the group average anatomic volume based on known anatomical distinctions (Bernasconi et al., 2003; Pruessner et al., 2002). An individual voxel threshold of $p < .001$ was enforced for all contrasts, whole-brain false discovery rate corrected for multiple comparisons to $p < .05$. False discovery rate correction for multiple comparisons ensures an acceptable rate of false positives across the entire brain for a given individual voxel threshold; thus, it does not require a minimal cluster extent (Logan & Rowe, 2004). All contrasts were weighted to account for differences in the number of each trial type. Activity within the medial temporal lobe was displayed on coronal slices. Activity in the other cortical regions was projected onto a sagittal slice or a representative inflated cortical surface (see Slotnick, 2005). Only data from retrieval were presented.

Event-related activation timecourses were extracted from each activation of interest within the time range of -2 to 12 sec after stimulus onset (baseline corrected from -2 to 0 sec). To avoid violation of independence, statistical analyses were based on the average activity from 6 to 8 sec after stimulus onset, the expected maximum of the hemodynamic response (Karanian & Slotnick, 2014a; Slotnick & Schacter, 2004).

3. Results

3.1. Behavioral results

Memory accuracy (i.e., percentage of hits, collapsed over confidence; chance = 50%) was at an intermediate level

(77.03% \pm 1.19%; Mean \pm 1 SE). As performance did not differ between shapes previously presented in the left visual field (75.50% correct) and shapes previously presented in the right visual field [78.60% correct; $t(15) < 1$], we collapsed over spatial location in the present analysis. The analysis included 193.69 \pm 3.45 true memory trials and 57.69 \pm 2.88 false memory trials (Mean \pm 1 SE). Table 1 shows the average percentage of responses for true memory and false memory as a function of confidence.

Table 1 – Behavioral Results. Percentage of each type of confidence response for true memory and false memory (mean \pm SE).

	“Unsure”	“Sure”	“Very Sure”
True memory	22.56 \pm 1.33	33.38 \pm 1.33	44.07 \pm 1.70
False memory	58.04 \pm 2.78	33.94 \pm 2.25	8.02 \pm 1.05

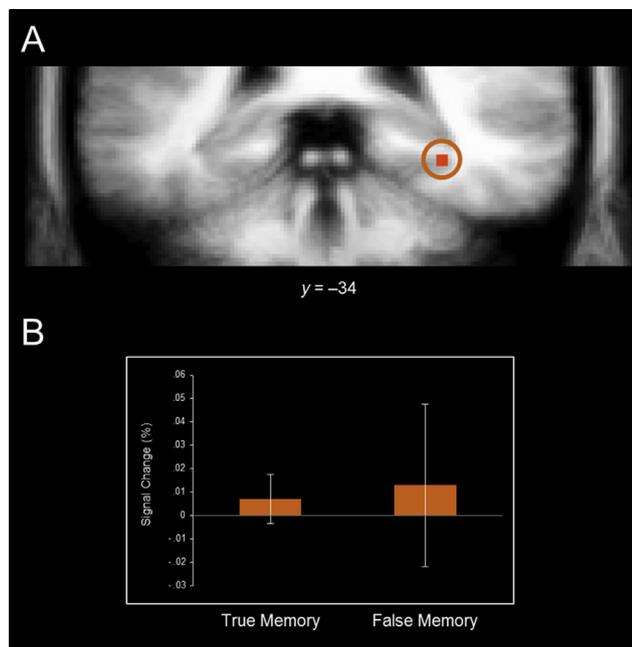


Fig. 2 – High/medium confidence true memory \cap high/medium confidence false memory activity in the parahippocampal cortex. A, Activity in the parahippocampal cortex (coronal view; activation is circled). B, True memory and false memory activity extracted from the parahippocampal cortex activation circled above.

3.2. True memory and false memory activity in the parahippocampal cortex

Next, we assessed whether high/medium confidence true memories for context and high/medium confidence false memories for context were mediated by similar regions of the parahippocampal cortex. Accordingly, we conducted the conjunction of high/medium confidence true memories for context and high/medium confidence false memories for context [i.e., (high/medium confidence true memories $>$ low confidence true memories) \cap (high/medium confidence false memories $>$ low confidence false memories)]. This conjunction produced activity in the parahippocampal cortex (Fig. 2A). Other context processing areas were also identified by this conjunction, including the hippocampus (Supplemental Fig. 1A) and the medial prefrontal cortex (Supplemental Fig. 1B). All activations within our regions of interest are listed in Table 2.

To distinguish between the visual-spatial processing view and the general contextual processing view, we extracted activity from the parahippocampal cortex activation identified by the above conjunction [i.e., (high/medium confidence true memories $>$ low confidence true memories) \cap (high/medium confidence false memories $>$ low confidence false memories)]. We then conducted an analysis of variance to evaluate the magnitudes of true memory and false memory activity in the parahippocampal cortex. As mentioned in the introduction, the visual-spatial processing view predicts that true memories will produce a greater magnitude of activity in the parahippocampal cortex than false memories (i.e., there will be a main effect of accuracy), whereas the general contextual processing view predicts that the magnitude of activity in the parahippocampal cortex will not differ between true memories and false memories (i.e., there will not be a main effect of memory accuracy). The interaction of memory accuracy (true memory, false memory) and confidence (high/medium, low) was not significant [$F(1, 15) < 1$], and there was no significant main effect of memory accuracy [true memory, false memory; $F(1, 15) < 1$]. Specifically, the magnitude of parahippocampal activity for true memories for context was .007 \pm .011 and the magnitude of activity for false memories for context was .014 \pm .035 (Fig. 2B).

It is possible that other regions of the parahippocampal cortex may have been preferentially associated with true memories for context as compared to false memories for context. To assess this possibility, we contrasted true memories for context and false memories for context (i.e.,

Table 2 – fMRI results. High/Medium Confidence True Memory \cap High/Medium Confidence False Memory Activations in regions of interest.

	Region x	y	Z	Size (mm ³)	Average t	Max. t
Medial prefrontal cortex	-14	31	26	2,214	3.25	3.59
Medial prefrontal cortex	-21	43	6	3,699	3.42	4.69
Medial prefrontal cortex	-18	43	3	189	2.48	2.86
Hippocampus	33	-25	-5	27	2.34	2.34
Parahippocampal cortex	30	-34	-8	27	2.33	2.33
Visual cortex	19	-84	0	3,591	2.84	5.59

Talairach coordinates (x, y, z) refer to the center of each activation. t refers to t-value.

high/medium/low confidence true memories > high/medium/low confidence false memories), which did not reveal any significant activity in the parahippocampal cortex. The reverse contrast (i.e., high/medium/low confidence false memories > high/medium/low confidence true memories) also produced null results in this region. Together, these contrasts suggest that true memories for context and false memories for context activated the parahippocampal cortex to a similar degree during retrieval.

We also assessed the extent of activity in the parahippocampal cortex that was associated with high/medium confidence true memories (i.e., high/medium confidence > low confidence true memories) and high/medium confidence false memories (i.e., high/medium confidence > low confidence false memories). In addition to the overlapping activity revealed by the conjunction of high/medium confidence true memories and high/medium confidence false memories, high/medium confidence true memories activated distinct regions of the parahippocampal cortex (Supplemental Fig. 2). It should be noted that the extent of activity associated with true memories was greater than the extent of activity associated with false memories.

3.3. True memory and false memory activity in visual cortical regions

The previous interpretations were based on the assumption that true memories for context were associated with greater visual-spatial detail than false memories for context in the present paradigm, which has been observed in many previous studies (Karanian & Slotnick, 2014a, 2017; Mather et al., 1997; Norman & Schacter, 1997; Slotnick & Schacter, 2004). However, proponents of the visual-spatial processing view could argue that the similar magnitudes of parahippocampal cortex activity for true memories and false memories resulted from similar degrees of visual-spatial detail in the current paradigm. To test this possibility, we assessed whether the conjunction of high/medium confidence true memories and high/medium confidence false memories produced activity in visual processing regions. This conjunction produced significant activity in right visual processing regions (Fig. 3A). We then extracted true memory activity and false memory activity from the most posterior activation (Fig. 3B). Analysis of this activity revealed a main effect of memory accuracy: the magnitude of activity associated with true memory ($.055 \pm .014$) was significantly greater than the magnitude of activity associated with false memory [$.006 \pm .020$; $F(1, 15) = 3.80, p < .05$, one-tailed]. Activity associated with true memory was significantly greater than baseline [$t(15) = 3.82, p < .005$], while activity associated with false memory did not significantly differ from baseline [$t(15) < 1$]. Furthermore, both activity associated with high/medium confidence true memory [$t(15) = 2.55, p < .05$] and low confidence true memory [$t(15) = 2.88, p < .01$] were significantly greater than baseline, while neither high/medium confidence false memory nor low confidence false memory differed significantly from baseline [both $t(15) < 1.57, ps > .14$]. These results indicate that there was greater visual-spatial processing during true memories than false memories.

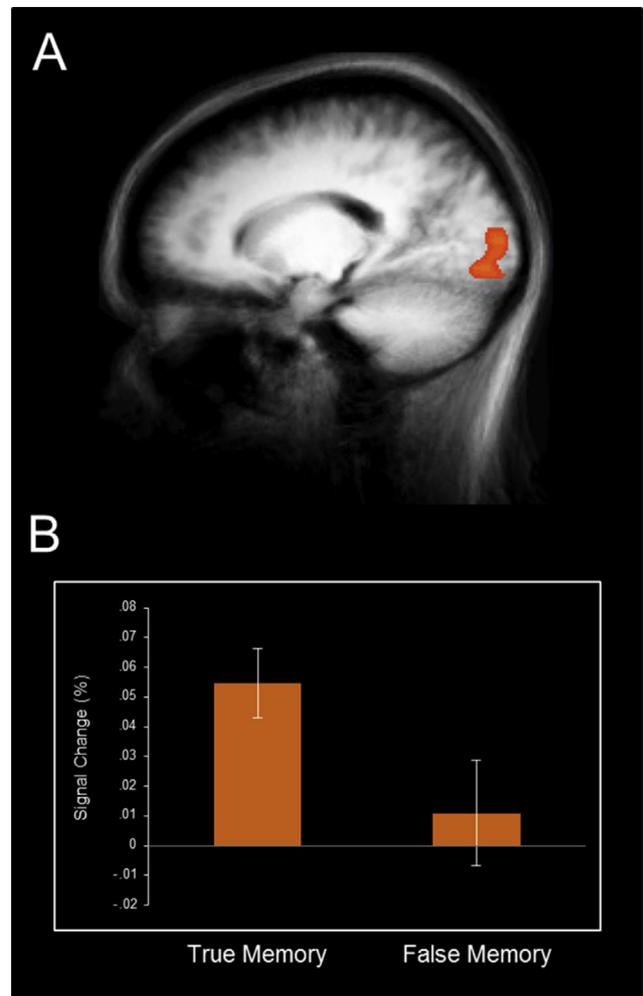


Fig. 3 – High/medium confidence true memory \cap high/medium confidence false memory activity in visual processing regions. A, Activity in visual processing regions (sagittal view of right hemisphere). B, True memory and false memory activity extracted from the activation shown above.

We also determined whether there were differences in visual processing regions using a direct contrast (i.e., high/medium/low confidence true memories > high/medium/low confidence false memories). The contrast of true memories for context and false memories for context produced significantly greater activity in V1 and extrastriate cortical regions (Supplemental Fig. 3). The reverse contrast (i.e., high/medium/low confidence false memories > high/medium/low confidence true memories) did not reveal any significant activity in visual processing regions. These findings provide additional evidence that true memories for context produced greater activity in visual processing regions than false memories for context and indicate that true memories were associated with a greater degree of visual-spatial processing in the present paradigm.

3.4. Parahippocampal cortex and visual cortex comparisons

The patterns of activity in the parahippocampal cortex (see Fig. 2B) and the visual cortex (see Fig. 3B) suggests that each

region has a unique functional role during retrieval. Thus, we also evaluated the magnitude of true memory and false memory activity in these regions. The magnitude of true memory activity in the visual processing region was significantly greater than the magnitude of activity in the parahippocampal cortex [$t(15) = 2.68, p < .01$], while the magnitude of false memory activity did not significantly differ between these regions [$t(15) < 1$].

4. Discussion

The comparison between the magnitude of true memory activity and false memory activity in the parahippocampal cortex is of particular relevance to the debate regarding the functional role of the parahippocampal cortex. Under the assumption that true memories are often associated with greater visual-spatial detail than false memories (Karanian & Slotnick, 2014a, 2017; Mather et al., 1997; Norman & Schacter, 1997; Slotnick & Schacter, 2004), the visual-spatial processing view predicts that true memories for context would produce a greater magnitude of parahippocampal activity than false memories for context. The general contextual processing view predicts that true memories for context and false memories for context would produce similar magnitudes of parahippocampal cortex activity. The conjunction analysis revealed that true memories for context and false memories for context produced similar magnitudes of parahippocampal cortex activity, which indicates that the parahippocampal cortex is not sensitive to differences in visual-spatial detail. The analogous analysis in visual regions produced differential activity for true memories for context and false memories for context. The present results indicate that the parahippocampal cortex is not sensitive only to visual-spatial information but rather is sensitive to contextual processing more generally during retrieval. This pattern of results directly contradicts the visual-spatial processing view.

The conjunction of confident true memories and confident false memories [i.e., (*high/medium confidence true memories* > *low confidence true memories*) \cap (*high/medium confidence false memories* > *low confidence false memories*)] produced activity in the parahippocampal cortex. This finding is consistent with previous results indicating that the parahippocampal cortex tracks the strength of subjective contextual processing (i.e., there is greater activity in this region during high confidence contextual processing than low confidence contextual processing). Specifically, in true memory studies (e.g., Diana, in press; Kirwan & Stark, 2004; Ranganath et al., 2004; Slotnick, 2013a, 2013b; Tendolkar et al., 2008), there has been greater parahippocampal cortex activity associated with high confidence memories as compared to low confidence memories. For instance, Tendolkar et al. (2008) demonstrated that retrieval-related activity in the parahippocampal cortex increased linearly based on the amount of context information retrieved. The present findings are also consistent with previous false memory results (Dennis et al., 2012; Karanian 2014b; but see; Abe et al., 2013). For example, Dennis et al. (2012) investigated neural differences associated with recollection-based false memory and familiarity-based false memory. These two types of false memory differ in

that recollection-based false memory involves the inaccurate retrieval of item and context information, while familiarity-based retrieval only involves inaccurate retrieval of item information. Such recollection-based false memories are similar to high/medium confidence false memories for context in the present study, as recollection has been shown to be highly correlated with high confidence judgments (Rotello, Macmillan, Reeder, & Wong, 2005; Slotnick, 2010a; Tulving, 1985). Similar to the present results, Dennis et al. (2012) demonstrated that recollection-based false memories were more associated with the parahippocampal cortex than familiarity-based false memories. Another fMRI study provided further evidence that false memories for context can produce activity in the parahippocampal cortex (Gershman, Schapiro, Hupbach, & Norman, 2013). Participants encoded two distinct lists of visual items. Critically, in addition to the items, list 1 also contained scene images. At retrieval, objects from list 1 and list 2 were presented and participants identified the previous context of each item (i.e., list 1 or list 2). Items from list 2 were misattributed to list 1 significantly more often than items from list 1 were misattributed to list 2. Retrieval-related activity in the posterior parahippocampal cortex was evaluated to determine whether reinstatement of the list 1 context (i.e., scene images) was associated with source misattributions for list 2 items. The magnitude of activity in the posterior parahippocampal cortex during retrieval predicted the confidence of these source misattributions. Such evidence is consistent with the present findings in which false memories were associated with activity in the parahippocampal cortex. In addition to the parahippocampal cortex, other cortical context processing regions (i.e., the hippocampus and the medial prefrontal cortex) were identified by the conjunction of high/medium confidence true memories and high/medium confidence false memories [i.e., (*high/medium confidence true memories* > *low confidence true memories*) \cap (*high/medium confidence false memories* > *low confidence false memories*)]. This is consistent with previous findings that these regions are important in contextual processing (e.g., Aminoff et al., 2013; Bar et al., 2008; Ranganath, 2010; Rugg & Vilberg, 2013; Slotnick, 2010b). Together with prior work, the present finding that confident memories for context were associated with activity in the parahippocampal cortex and other context processing regions suggests that the parahippocampal cortex tracks the subjective strength of memories for context. Such evidence provides support for the general contextual processing view.

It is noteworthy that proponents of the visual-spatial processing view have pointed to the inconsistency of results supporting the contextual processing view of the parahippocampal cortex (Epstein & Ward, 2010). That is, a number of studies investigating true memory for context have failed to identify parahippocampal cortex activity when comparing accurate context memory and inaccurate context memory. For instance, within the visual modality, Peters, Suchan, Koster, and Daum (2007) contrasted accurate and inaccurate context memories, which did not produce significant activity in the parahippocampal cortex. However, upon examination of the timecourses extracted from the parahippocampal cortex, the null results did not appear to be driven by a lack of activity in the parahippocampal cortex during accurate

context memories but rather may be attributable to an increase in parahippocampal cortex activity for inaccurate context memories. That is, accurate and inaccurate memories appear to have activated the parahippocampal cortex to a similar degree. In the paradigm employed by Peters et al. (2007), inaccurate context memories were similar to false memories for context, as incorrect context memories were defined as attributing an old item to the wrong context (i.e., auditory context vs visual context; cf., Karanian & Slotnick, 2014b). Such evidence indicates that true memories for context and false memories for context can activate the parahippocampal cortex to a similar degree, which may explain some of the null findings within the parahippocampal cortex literature. This is a topic for future research.

There is some fMRI evidence that suggests the parahippocampal cortex varies in function along the anterior–posterior axis. The anterior parahippocampal cortex has been preferentially associated with retrieval of contextual information (e.g., Epstein, 2008; Ekstrom & Bookheimer, 2007; Xu, Evensmoen, Lehn, Pintzka, & Haberg, 2010), while the posterior parahippocampal cortex has been preferentially associated with perception of contextual information (e.g., Epstein, 2008; Epstein & Kanwisher, 1998; Epstein et al., 1999). In the present study, our analyses identified retrieval-related activity within the posterior parahippocampal cortex. Thus, our findings are in line with the view that perception- and memory-related contextual processing can be mediated by both anterior and posterior aspects of the parahippocampal cortex (Aminoff, Gronau, & Bar, 2007).

The behavioral literature has also investigated the mechanism that supports the construction of highly confident false memories in old-new recognition/Deese-Roediger-McDermott (DRM) paradigms in which participants falsely remember related lures as old (Roediger & McDermott, 2005). One theory that has emerged to explain such high confidence false memories is content borrowing (Lampinen, Meier, Arnal, & Leding, 2005; Lampinen, Ryals, & Smith, 2008). Lampinen et al. (2005; 2008) have demonstrated that as many as half of vivid false memories produced in DRM paradigms can be attributed to content borrowing, such that details associated with old items were misattributed to lures during retrieval. Content borrowing may help to explain the occurrence of some instances of false memory in the present study. Specifically, the conjunction of confident true memories and confident false memories [i.e., (*high/medium confidence true memories* > *low confidence true memories*) \cap (*high/medium confidence false memories* > *low confidence false memories*)] produced activity in visual processing regions, which suggests that content borrowing may have occurred during confident false memories. For instance, it is possible that a shape previously presented in the right visual field was similar to a shape that was previously presented in the left visual field, and such similarity may have induced reinstatement of the incorrect context during retrieval. If this were generally the case for false memories in the present study, similar reinstatement patterns would have been observed in visual processing regions for confident true memories and confident false memories. However, we also found that true memories produced greater activity in visual processing regions than false memories. Nonetheless, it remains possible that content borrowing

may explain some of the confident false memories observed in the present study. This is a topic of future research.

5. Conclusions

In the present study, we found that true memories for context and false memories for context similarly activated the parahippocampal cortex. Furthermore, we found that true memories for context activated visual processing regions to a greater degree than false memories for context. This evidence supports the view that the parahippocampal cortex mediates general processing of contextual information rather than specific visual-spatial processing. Future studies should implement paradigms in which the context is devoid of visual-spatial processing, such as nonspatial (e.g., color) or nonvisual (e.g., auditory) contexts. It is predicted that such studies will provide additional support for the view that the parahippocampal cortex is associated with general contextual processing rather than visual-spatial processing.

Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.02.007>.

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