CORTEX 91 (2017) 79–88

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Special issue: Research report

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

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ARTICLE INFO

Article history:
Received 26 June 2016
Reviewed 5 August 2016
Revised 26 September 2016
Accepted 7 February 2017
Published online 24 February 2017

Keywords:
False recollection
fMRI
Source memory
Spatial memory
True memory

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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http://dx.doi.org/10.1016/j.cortex.2017.02.007
0010-9452/

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 Turennout, 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