Neuropsychologia 51 (2013) 2322–2332

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Medial temporal lobe contributions to cued retrieval of items and contexts

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ARTICLE INFO

Available online 1 March 2013

Keywords:
Episodic memory
Retrieval
Medial temporal lobe
Perirhinal cortex
Parahippocampal cortex
Hippocampus

ABSTRACT

Several models have proposed that different regions of the medial temporal lobes contribute to different aspects of episodic memory. For instance, according to one view, the perirhinal cortex represents specific items, parahippocampal cortex represents information regarding the context in which these items were encountered, and the hippocampus represents item–context bindings. Here, we used event-related functional magnetic resonance imaging (fMRI) to test a specific prediction of this model—namely, that successful retrieval of items from context cues will elicit perirhinal recruitment and that successful retrieval of contexts from item cues will elicit parahippocampal cortex recruitment. Retrieval of the bound representation in either case was expected to elicit hippocampal engagement. To test these predictions, we had participants study several item–context pairs (i.e., pictures of objects and scenes, respectively), and then had them attempt to recall items from associated context cues and contexts from associated item cues during a scanned retrieval session. Results based on both univariate and multivariate analyses confirmed a role for hippocampus in content-general relational memory retrieval, and a role for parahippocampal cortex in successful retrieval of contexts from item cues. However, we also found that activity differences in perirhinal cortex were correlated with successful cued recall for both items and contexts. These findings provide partial support for the above predictions and are discussed with respect to several models of medial temporal lobe function.

1. Introduction

It is not an uncommon experience to come across an item that triggers memory for related contextual information or a context that calls to mind a particular item. For example, while rummaging through a junk drawer, you might encounter a shell amongst the rubble and immediately recall the beach where you enjoyed your first surfing lesson. Conversely, you might happen upon that beach sometime later, and be reminded of the shell you kept from your surfing experience. While both of these examples illustrate the act of retrieving additional information from a particular cue (i.e., either context from item or item from context), they may differentially engage brain regions known to play a critical role in successful encoding and subsequent retrieval of episodic memories.

There is broad consensus that the medial temporal lobes (MTL) are critical for long-term memory, and several models have proposed that the hippocampus and adjacent MTL cortical structures (e.g., the perirhinal and parahippocampal cortices) contribute in different ways (e.g., Brown & Aggleton, 2001; Cohen & Eichenbaum, 1993; Davachi, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; Graham, Barense, & Lee, 2010). According to one influential model, perirhinal cortex supports the process of familiarity-based recognition, and the hippocampus supports successful recollection (Brown & Aggleton, 2001). Competing models have stressed differences in the representational characteristics of MTL structures, emphasizing a role for the hippocampus in relational memory (e.g., memory for relationships among items and the contexts in which they were initially encountered; Cohen & Eichenbaum, 1993) and roles for the perirhinal and parahippocampal cortices in representation of information about items and contexts, respectively (e.g., Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Eacott & Gaffan, 2005; Eichenbaum et al., 2007; Montaldi & Mayes, 2010).

As emphasized in one of these models – the Binding of Items and Context (or BIC) model (Diana et al., 2007; Eichenbaum et al., 2007) – process-based and representational views are not necessarily incompatible because hippocampus-mediated relational memory representations may support the experience of recollection (i.e., item recognition accompanied by successful retrieval of additional details about the encoding context) and item-specific perirhinal representations may support a subjective sense of familiarity (i.e., item recognition absent any associated information about the encoding experience). Importantly, however, the

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.02.011

BIC model does not rule out possible contributions of perirhinal cortex to recollection, which is consistent with results of recent functional magnetic resonance imaging (fMRI) investigations showing that perirhinal cortex contributes to successful source recollection when source (in this example, a particular color) has been encoded as an item detail (e.g., a red elephant; Staresina & Davachi, 2008). The BIC model also predicts that activity differences in the parahippocampal cortex will be associated with successful recollection to the extent that contextual representations have been recovered.

The fMRI experiment described here was designed to test a specific prediction of the BIC model—namely that cued recall of items from contexts will elicit perirhinal recruitment and that cued recall of contexts from items will elicit parahippocampal recruitment. To test this prediction, we had participants encode trial unique item–context pairs where items were pictures of common objects and contexts were pictures of indoor and outdoor scenes. During a scanned retrieval phase, participants attempted to recall contexts (i.e., studied scenes) from associated item cues and to recall items (i.e., studied objects) from associated context cues. Univariate and multivariate (i.e., pattern similarity) approaches were used to identify BOLD signal changes correlated with successful cued retrieval of items and contexts. These effects were evaluated in contrasts that compared studied cues for which the associate was successfully recalled to studied cues that were merely endorsed as familiar. In addition to predicted effects for the perirhinal and the parahippocampal cortices, we expected that successful cued recall in either condition, both of which required recovery of item–context relationships, would be supported by BOLD signal changes in the hippocampus.

2. Methods

2.1. Participants

Twenty-nine individuals (20 females) from the UC Davis community participated in this experiment and were compensated at a rate of 20 dollars per hour for their time. Data from 11 of these individuals were excluded because the number of trials (i.e., at least 8 per bin) associated with conditions of interest was insufficient for fMRI analyses or because of technical difficulties; therefore, the reported results reflect data from 18 participants (12 females). Informed consent was obtained from each individual in a manner approved by the Institutional Review Board at the University of California, Davis.

2.2. Materials

Materials included 228 items (pictures of objects—e.g., cardboard box, bandana, boomerang) and 228 contexts (full-color scenes—e.g., beach, auditorium). Because past work has shown that items with strong pre-experimental links to particular contexts (e.g., a filing cabinet) may automatically elicit retrieval of those contexts (e.g., Bar & Aminoff, 2003), we made every effort to select items for which this would not be the case. In addition, we were careful to select distinctive scene contexts from a variety of categories (e.g., there was just one bedroom scene, and contexts also included a pool hall, a cave, and a warehouse). Based on these methodological choices, it is unlikely that pre-experimental congruence between items and contexts would influence the reported outcomes.

From the above set of materials, 12 items and 12 contexts were used during a practice phase that was administered prior to the experiment. Items were sized to 150×150 pixels including a 10 pixel gray border and contexts were sized to 400×300 pixels including a 10 pixel white border; total screen resolution was set to 800×600 pixels.

2.3. Procedure and design

After informed consent was obtained from each participant, the experimenter provided instructions in step with a 3-phase practice session. The practice session was an abbreviated version of the experiment proper and consisted of an encoding phase, a retrieval phase, and a post-test. When the experimenter was satisfied that the participant understood all of the instructions, and any remaining questions had been answered, the experiment commenced.

During the encoding phase, which took place outside of the scanner, participants were asked to commit 180 trial-unique item–context pairs to memory. Each pair remained in view for 3500 ms, and was followed by a screen prompting participants to indicate whether or not they had successfully generated a story about how the item might be used in the associated context; this response requirement was meant to encourage active processing of each item–context pair. The prompt remained on the screen until a button press was made, and was then replaced with a centrally-located fixation cross that was visible for 1000 ms before the next trial was initiated (see Fig. 1a). All of the studied pairs were presented in a single block of trials.

A scanned retrieval phase, consisting of six runs, took place shortly after encoding. During retrieval, individual pictures of items and contexts were presented for 2000 ms in random order and participants were instructed to use these pictures as cues in an attempt to recall studied associates. There were 48 trials per run—36 of these were retrieval trials and the remainders were active baseline trials that are not considered further in this report. A prompt, the word "Remember", preceded each picture by 2000 ms and distinguished retrieval trials from baseline trials; the mean inter-trial interval was 6000 ms (range= 4000–8000 ms). Pictures used in two-thirds of the retrieval trials were from studied pairs (12 studied items and 12 studied contexts per run; 72 of each total) and the remainders were novel (6 novel items, 6 novel contexts; 36 of each total). Importantly, if one element from a studied pair was presented as a retrieval cue, its associate was not.

Upon presentation of each picture, participants were instructed to make *new* responses if they felt the picture had not been seen during the corresponding

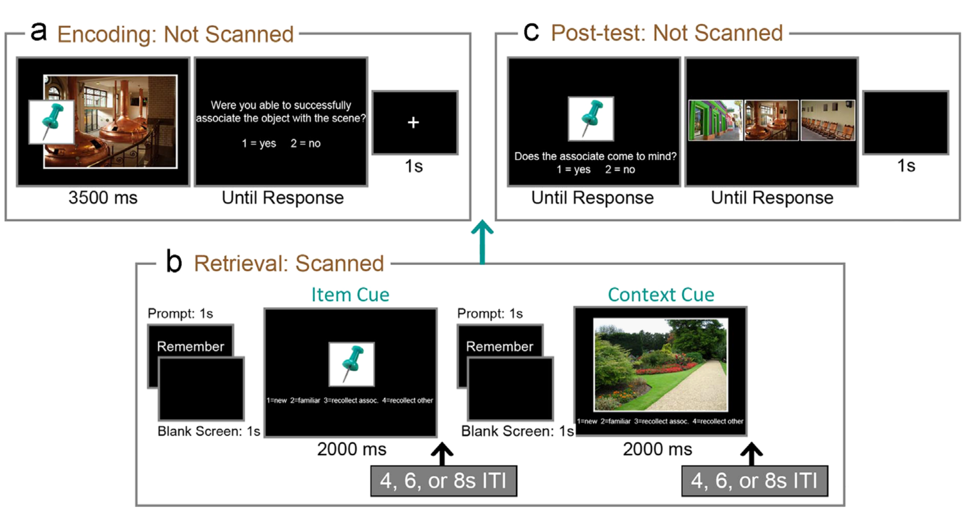

Fig. 1. Illustration of materials and methods. A representative item–context pair (a) is presented along with associated trials from the scanned retrieval phase (b) and the unscanned post-test (c). In this example the thumbtack is a *studied* item cue and the garden path is a *novel* scene cue. Studied scene cues and novel item cues were also presented during the scanned retrieval phase, but are not illustrated here.