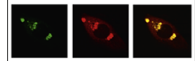


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Research Report

Source recognition by stimulus content in the MTL



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ABSTRACT

Source memory is considered to be the cornerstone of episodic memory that enables us to discriminate similar but different events. In the present fMRI study, we investigated whether neural correlates of source retrieval differed by stimulus content in the medial temporal lobe (MTL) when the item and context had been integrated as a perceptually unitized entity. Participants were presented with a list of items either in verbal or pictorial form overlaid on a colored square and instructed to integrate both the item and context into a single image. At test, participants judged the study status of test items and the color in which studied items were presented. Source recognition invariant of stimulus content elicited retrieval activity in both the left anterior hippocampus extending to the perirhinal cortex and the right posterior hippocampus. Word-selective source recognition was related to activity in the left perirhinal cortex, whereas picture-selective source recognition was identified in the left posterior hippocampus. Neural activity sensitive to novelty detection common to both words and pictures was found in the left anterior and right posterior hippocampus. Novelty detection selective to words was associated with the left perirhinal cortex, while activity sensitive to new pictures was identified in the bilateral hippocampus and adjacent MTL cortices, including the parahippocampal, entorhinal, and perirhinal cortices. These findings provide further support for the integral role of the hippocampus both in source recognition and in detection of new stimuli across stimulus content. Additionally, novelty effects in the MTL reveal the integral role of the MTL cortex as the interface for processing new information. Collectively, the present findings demonstrate the importance of the MTL for both previously experienced and novel events.

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1. Introduction

Recognition of a previously encountered event can be based on remembering the event with its contextual details (recollection) or an acontextual sense of prior occurrence of the event (familiarity) (Mandler, 1980; Yonelinas, 2002). Medial temporal lobe (MTL) subregions differ in their contribution to recollection and familiarity. That is, the hippocampus makes

critical contributions to recollection but not familiarity, and the parahippocampal cortex is particularly involved in recollection of source information. However, the perirhinal cortex is thought to be related to familiarity (Brown and Aggleton, 2001; Holdstock et al., 2005; Manns and Eichenbaum, 2006). MTL subregions also differ in the types of stimulus content that they process (Awipi and Davachi, 2008; Graham et al., 2010; Lee et al., 2008; Liang et al., 2013; Taylor et al., 2007;

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Watson et al., 2012). Given that associations mediated by the hippocampus have been found with different types of stimuli, the hippocampus is considered to play more of a general role in association of items and contexts across content (Cansino et al., 2002; Davachi et al., 2003; Duarte et al., 2011; Staresina et al., 2011). Other regions tend to take more specific roles in terms of stimulus content: the parahippocampal cortex is recruited for visuo-spatial processing, whereas the perirhinal cortex is linked to object processing (Awipi and Davachi, 2008; Ekstrom and Bookheimer, 2007; Staresina et al., 2011; Wolbers and Büchel, 2005). Based on the role of the perirhinal cortex in object processing, it has been proposed that source memory for objects can be mediated by perirhinal activity, especially when the context is processed as a feature of the object (Diana et al., 2007; Ranganath, 2010).

While previous fMRI studies have provided useful information about neural activity related to content-selective source recognition, they have mostly used semantic tasks for examining neural correlates of contextual associations during retrieval that depend on content (Duarte et al., 2011; Dulas and Duarte, 2012). A semantic task for the formation of contextual associations is more likely to demand semantic processing of the to-be-remembered material. Previous neuroimaging studies of memory have shown that neural correlates of memory dissociate semantic and non-semantic memory (Otten and Rugg, 2001; Park et al., 2008), and these findings suggest that source memory with a semantic task may recruit neural correlates that are different from the neural correlates of source memory with a non-semantic task. While the semantic task provides an important path for encoding and retrieval of contextual associations, fMRI examinations of content-selective source recognition with non-semantic tasks are lacking.

Further, the results on content-selective effects on source recognition were rather mixed (e.g., Duarte et al., 2011), although hippocampal activity was reported for source recognition common to different stimulus content. When an object-based perceptual encoding task was used, perirhinal activity was related to source memory for objects, while parahippocampal activity predicted source memory for scenes, thereby revealing content-selective source encoding effects in the MTL cortex between two types of pictorial content (Staresina et al., 2011). Yet, it has not been established if content-selective source effects appear during retrieval when contextual associations are formed via object-based encoding, especially between verbal and pictorial content. Previous EEG studies demonstrated that words and pictures showed different congruency effects or different frontal effects (Bauch and Otten, 2012; Galli and Otten, 2011), and subsequent associative memory effects also dissociated between word and picture pairs (Park and Rugg, 2011). These findings suggested that neural correlates of content-selective effects occurred mainly between verbal and pictorial content. Based on these findings, the present study examined content-selective effects in source recognition by employing words and pictures. Object processing with words may require neural correlates that are different from object processing with pictures, considering that the generation of object representations from words may require additional processing than the generation of object representations from

pictures due to the difference in the sensory process or the process match effects (Kinjo and Snodgrass, 2000). Alternatively, it is also plausible that both words and pictures recruit common neural correlates for source recognition as they form an integrated object representation and retrieve the representation regardless of content. Thus, it is of interest whether source recognition of words and pictures via object-based processing would show content-selective effects of source retrieval.

The MTL including the hippocampus is known to be sensitive to detecting the presence of novel stimuli (O'Kane et al., 2005; Stark and Okado, 2003). However, it has not yet been fully understood whether MTL novelty effects differ according to the content of new stimuli that are presented with studied stimuli during source recognition. On item recognition tests, the new items that were correctly judged as “new” (correct rejections) tended to elicit greater MTL activity than did the studied items that were correctly judged as “old” (hits) (Daselaar et al., 2006; Dudukovic and Wagner, 2007; O'Kane et al., 2005; Yu et al., 2012). These novelty detection effects have been interpreted as an MTL-mediated encoding process for new stimuli at test (Rugg et al., 2012; Stark and Okado, 2003). The hippocampus is sensitive to detection of new stimuli among studied stimuli between study and test, and the adjacent MTL cortex also tends to be sensitive to the difference between first-presented items versus repeated items on continuous recognition (Howard et al., 2011; Yassa and Stark, 2008). In light of content-selective functions of MTL subregions, it would be of interest to see if novelty detection effects between study and test also reveal differences of MTL subregions depending on stimulus content.

The present event-related fMRI addressed the question of whether retrieval of source memory elicits neural activity selective to stimulus content within the MTL. To this end, we manipulated the type of stimulus content (verbal vs. pictorial) with perceptual context (4 colors) through integrated contextual associations. Participants were presented an object either as a word or a picture in one of four color squares during study. To facilitate the formation of item-context associations, participants were instructed to form an image of the object in the color. During test, participants were presented stimuli without color and were asked to make source recognition judgments. For studied stimuli, content type was kept constant between study and test.

We first examined if source retrieval effects invariant of content would emerge in the hippocampus through integrated contextual associations. We hypothesized that source retrieval effects invariant of content would emerge in the hippocampus, as hippocampal source recognition effects have been found across different materials, tasks, and contexts. Second, we investigated if content-selective source retrieval effects would occur when both words and pictures underwent the same study task. We suspected that a greater emphasis would be placed on processing the word as an object in the word condition than in the picture condition. We hypothesized that content-selective source recognition effects would be found in different MTL regions, as it was more likely that the word with accurate source information had been processed as an object than the word without

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