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Medial temporal lobe reinstatement of content-specific details predicts source memory

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ABSTRACT

Leading theories propose that when remembering past events, medial temporal lobe (MTL) structures reinstate the neural patterns that were active when those events were initially encoded. Accurate reinstatement is hypothesized to support detailed recollection of memories, including their source. While several studies have linked cortical reinstatement to successful retrieval, indexing reinstatement within the MTL network and its relationship to memory performance has proved challenging. Here, we addressed this gap in knowledge by having participants perform an incidental encoding task, during which they visualized people, places, and objects in response to adjective cues. During a surprise memory test, participants saw studied and novel adjectives and indicated the imagery task they performed for each adjective. A multivariate pattern classifier was trained to discriminate the imagery tasks based on functional magnetic resonance imaging (fMRI) responses from hippocampus and MTL cortex at encoding. The classifier was then tested on MTL patterns during the source memory task. We found that MTL encoding patterns were reinstated during successful source retrieval. Moreover, when participants made source misattributions, errors were predicted by reinstatement of incorrect source content in MTL cortex. We further observed a gradient of content-specific reinstatement along the anterior–posterior axis of hippocampus and MTL cortex. Within anterior hippocampus, we found that reinstatement of person content was related to source memory accuracy, whereas reinstatement of place information across the entire hippocampal axis predicted correct source judgments. Content-specific reinstatement was also graded across MTL cortex, with PRc patterns evincing reactivation of people and more posterior regions, including PHc, showing evidence for reinstatement of places and objects. Collectively, these findings provide key evidence that source recollection relies on reinstatement of past experience within the MTL network.

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1. Introduction

The ability to recall details about prior experiences—such as their origin or source—is thought to rely on reinstatement of the neural patterns active during initial encoding (for a review see Davachi & Preston, 2015). Leading theories suggest that during recollection, the hippocampus and surrounding medial temporal lobe (MTL) cortex mediate reinstatement of memory representations in response to partial cues—a process known as pattern completion (McClelland, McNaughton, & O'Reilly, 1995; Norman & O'Reilly, 2003). In turn, reinstatement within the MTL network is thought to drive reinstatement of the corresponding cortical activation patterns associated with an original experience, allowing for recollection of event details. While several studies have shown that cortical reinstatement tracks source memory (Bird, Keidel, Ing, Horner, & Burgess, 2015; Bosch, Jehee, Fernandez, & Doeller, 2014; Gordon, Rissman, Kiani, & Wagner, 2014; Johnson, McDuff, Rugg, & Norman, 2009; Kuhl & Chun, 2014; Morcom, 2014; Thakral, Wang, & Rugg, 2015; Wheeler, Petersen, & Buckner, 2000; Wing, Ritchey, & Cabeza, 2015), a direct link between MTL reinstatement and successful source retrieval has been more elusive.

Electrophysiological work in humans has shown that individual MTL neurons active during encoding of short episodes fire again when those episodes are recalled (Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008), with activity predicting both recognition strength and confidence (Rutishauser et al., 2015). Consistent with these human studies, physiological recordings in rodents have shown reactivation of hippocampal activity patterns during retrieval (for a review see Carr, Jadhav, & Frank, 2011). For instance, hippocampal cells representing a movement trajectory through a well-learned environment are replayed in sequence at remote time points (Karlsson & Frank, 2009). Interrupting such hippocampal replay impairs navigational ability in rodents (Jadhav, Kemere, German, & Frank, 2012). Collectively, these findings indicate that reinstatement of MTL memory representations plays an important role in guiding behavior and choice. However, these findings do not speak directly to the role of MTL reinstatement in the accurate retrieval of detailed source information.

In contrast to electrophysiological research, evidence for MTL reinstatement during retrieval as measured by functional magnetic resonance imaging (fMRI) has been limited. Recent work has shown that the magnitude of hippocampal activation during retrieval is associated with the speed (Gordon et al., 2014) and confidence (Leiker & Johnson, 2015; Thakral et al., 2015) of memory decisions. Several studies have further shown that hippocampal engagement during both encoding (Danker, Tompary, & Davachi, 2016) and retrieval is correlated with measures of cortical reinstatement at test (Bosch et al., 2014; Horner, Bisby, Bush, Lin, & Burgess, 2015; Leiker & Johnson, 2015; Ritchey, Wing, Labar, & Cabeza, 2013; Wing et al., 2015). Thus, while these studies suggest a link between MTL processing, cortical reinstatement, and successful retrieval, they do not provide evidence for retrieval-related MTL reinstatement per se.

Studies that have observed reinstatement of MTL encoding patterns during retrieval do not always see a link with memory behavior (Wimber, Alink, Charest, Kriegeskorte, & Anderson, 2015). Two notable exceptions have shown performance-related reinstatement of specific memory content in hippocampus, perirhinal cortex (PRc), and parahippocampal cortex (PHc) (Mack & Preston, 2016; Staresina, Henson, Kriegeskorte, & Alink, 2012). In one of these studies, PHc encoding patterns for word-scene associations were reinstated when participants recalled the correct scene in response to its associated word cue (Staresina et al., 2012). A more recent study (Mack & Preston, 2016) combined high-resolution fMRI with a multivariate decoding approach designed to index retrieval of specific items. Mack and colleagues provided evidence for reinstatement of specific faces in PRc and specific scenes in hippocampus during recall, with the fidelity of MTL reinstatement predicting the speed of memory decisions. However, memory performance in that study was near ceiling, limiting the connection between MTL reinstatement and the accuracy of source retrieval. A major goal of the present study is to test the prediction that MTL reinstatement should not only predict correct source retrieval, but also track the pattern of source memory errors. If there is a strong link between MTL reinstatement and source decisions, activation patterns reflecting reinstatement of incorrect source content should lead to source misattributions.

A second goal of the present study is to test the hypothesis that distinct MTL subregions support reinstatement of specific kinds of source content. Leading theories suggest that hippocampus, PRc, and PHc play unique roles in memory that depend on the content of experience (Bird & Burgess, 2008; Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Ritchey, Libby, & Ranganath, 2015). One perspective suggests that PRc and PHc mediate encoding and retrieval of visual object (including faces) and visuospatial information respectively, while hippocampus plays a content-general role in memory (Davachi, 2006; Diana et al., 2007). An alternative account proposes that hippocampus may play a specialized role in visuospatial memory, as hippocampal lesions result in deficits in place, but not face memory (Bird & Burgess, 2008). Recent data further indicate that there may be functional differentiation within hippocampus, as anterior hippocampus shows preferential connectivity with PRc and posterior hippocampus with PHc (Libby, Ekstrom, Ragland, & Ranganath, 2012). This observation and others (Liang, Wagner, & Preston, 2013) suggest that while posterior hippocampus may mediate memory for visuospatial information, anterior hippocampus may be more sensitive to visual object content or show domain-general memory responses. Prior studies indexing MTL representation at encoding and retrieval have revealed content-based dissociations across MTL subregions (Diana, Yonelinas, & Ranganath, 2008; Huffman & Stark, 2014; Liang et al., 2013; Mack & Preston, 2016; Staresina et al., 2012). Here, we examine how such specialization relates to source memory, by indexing reinstatement of person, place, and object source information along the longitudinal axis of both hippocampus and MTL cortex.

During incidental encoding, participants were cued to visualize a person, place, or object characterized by a presented adjective. During a surprise source memory task, participants saw studied and novel adjectives and indicated which imagery task they performed for each adjective or if an adjective was new. A neural classifier was trained to