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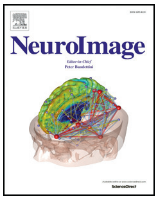

Decisions about the past are guided by reinstatement of specific memories in the hippocampus and perirhinal cortex

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A B S T R A C T

When faced with a new challenge, we often reflect on related past experiences to guide our behavior. The ability to retrieve memories that overlap with current experience, a process known as pattern completion, is theorized as a critical function of the hippocampus. Although this view has influenced research for decades, there is little empirical support for hippocampal pattern completion to individual memory elements and its influence on behavior. We used pattern analysis of brain activity measured with functional magnetic resonance imaging to demonstrate that specific elements of past experiences are reinstated in the hippocampus, as well as perirhinal cortex (PRC), when making decisions about those experiences. Linking neural measures of specific memory reinstatement in the hippocampus and PRC to behavior with computational modeling revealed that reinstatement predicts the speed of memory-based decisions. Moreover, hippocampal activation during retrieval was selectively coupled to regions of occipito-temporal cortex that showed content-specific item reinstatement. These results provide evidence for hippocampal pattern completion and its role in the mechanisms of decision making.

Decisions often rely on information that is not immediately available. Whether it is ordering an entrée at a favorite restaurant or deciding among treatment options for a medical condition, many of our decisions are guided by what we recall from past experience. Most research on the neural systems of decision making have focused on perceptual decisions that depend on information directly or recently available to the sensory system (Heekeren et al., 2008). Although such studies have characterized how external sensory information is represented and interpreted by the brain to influence behavior (Bogacz et al., 2010; Bollimunta et al., 2012; Gold and Shadlen, 2007; Hanks et al., 2014; Heekeren et al., 2008; Nienborg and Cumming, 2009), the neural computations that support how we use internally-generated content from past experiences to guide decision making remain poorly understood.

It is well known that our ability to encode and remember past experiences depends critically on the medial temporal lobe (MTL) (Eichenbaum, 2004; Squire, 2004). The prominent theoretical view (Marr, 1971; McClelland et al., 1995; O'Reilly and Rudy, 2001) proposes that successful memory retrieval involves reinstatement of memory representations through a process known as pattern completion. Specifically, the hippocampus is thought to act as an auto-associative network that reinstates complete memory representations from partial or degraded input. It has been further proposed that the content of these reinstated memories serve as internally-generated evidence that guides subsequent behavior (Lisman and Grace, 2005; Norman and O'Reilly, 2003). In the present study, our goal was to test the theoretical prediction that during memory-based decision making, specific memory elements are reinstated in the human hippocampus and that this reinstatement predicts decisions.

Empirical evidence for hippocampal memory reinstatement and its influence on decision making has been established in human electrophysiological studies. This work has demonstrated that firing patterns of single neurons in medial temporal lobe selectively code for specific contents of memory (Heit et al., 1988) and that reinstatement of these firing patterns during retrieval is related to memory performance (Gelbard-Sagiv et al., 2008; Paz et al., 2010; Rutishauser et al., 2015). However, such empirical evidence of pattern completion in human functional magnetic resonance imaging (fMRI) research has been limited. Initial reports focused on differences in process rather than contents of memories, inferring pattern completion from a reduction in blood-oxygen-level dependent (BOLD) response to repeated presentations of objects and similar lures relative to initial encoding (Bakker et al., 2008; Lacy et al., 2011). Such an effect is consistent with pattern completion; however, it is unknown whether or not such reduced neural responding reflects reinstatement of specific memory elements.

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fMRI studies have demonstrated that hippocampal activation patterns during spatial context encoding exhibit a bias towards existing spatial templates, a finding consistent with pattern completion processes (Stokes et al., 2015). Further, it has been shown that hippocampal activation patterns during retrieval differentiate between stored event representations (Chadwick et al., 2010, 2011) and are consistent with episode-specific templates of activation patterns recorded after encoding and retrieval (Wimber et al., 2015). However, these extant findings cannot speak to the central tenet of pattern completion: hippocampal activation patterns representing specific memory elements are themselves reinstated during decisions that rely on memory.

A second theoretical aspect of pattern completion with limited empirical support is the proposal that reinstated mnemonic information in the hippocampus serves as evidence for memory-based decision making (Lisman and Grace, 2005; Norman and O'Reilly, 2003). It has been demonstrated that successful memory decisions are associated with stronger reinstatement signatures in content-specific cortical regions (Bosch et al., 2014; Johnson et al., 2009; Kuhl and Chun, 2014; LaRocque et al., 2013; Polyn et al., 2005; Ritchey et al., 2012; Staresina et al., 2012; Wing et al., 2015). However, the behavioral link between memory decisions and hippocampal pattern completion has yet to be observed. Furthermore, the link between reinstatement and behavior observed in these studies is based on the indirect comparison of cortical reinstatement signatures during successful versus unsuccessful memory choices, thus limiting the sensitivity of evaluating the direct influence of reinstatement on decision making on a trial-by-trial basis. Recent neuroimaging evidence shows that the magnitude of hippocampal activation is linked to memory confidence judgments (Leiker and Johnson, 2015; Thakral et al., 2015) and the speed of memory decisions (Gordon et al., 2014), with greater retrieval-related activation for higher confidence and faster responses. Electrophysiological work in humans has further identified single cells within the hippocampus that exhibit firing patterns consistent with a graded representation of memory strength and confidence during recognition decisions (Rutishauser et al., 2015). However, these studies did not index hippocampal pattern completion per se. And, although the single cell finding is a compelling demonstration of hippocampal cells representing memory evidence, the kind of information carried by these cells was not item specific, and the memory-specific firing patterns were observed in response to perceptual information currently available to the participant. The theoretically important question remains as to whether or not internally generated hippocampal memory evidence is directly related to decisions about the specific mnemonic content.

Here, we sought direct evidence of pattern completion during memory-based decision making by indexing reinstatement of the specific components of individual memories from patterns of fMRI activation in the human hippocampus and surrounding cortices. Participants learned arbitrary associations between pictures of objects and famous faces and places before performing a delayed match-to-memory test (Chen et al., 2011), in which objects cued memory retrieval of the associated face or place (Fig. 1). We used neural pattern similarity (Kriegeskorte et al., 2008; Xue et al., 2010) to assess the reinstatement of specific people and places during memory retrieval in parahippocampal cortex (PHC) and perirhinal cortex (PRC), MTL cortical regions that have demonstrated content-specific coding (e.g., LaRocque et al., 2013; Liang et al., 2013; Staresina et al., 2012), and hippocampus (Fig. 1). Item-specific patterns during retrieval were compared to item-specific neural patterns recorded during a pre-exposure phase, in which participants viewed each item in isolation prior to associative encoding. This approach allowed us to go beyond category level decoding of memory reinstatement (Johnson et al., 2009; Polyn et al., 2005), a method that has failed to provide evidence for reinstatement of hippocampal representations (Diana et al., 2008; Gordon et al., 2014; cf. Kuhl and Chun, 2014), to assess reinstatement of specific memory elements.

Furthermore, we investigated the theoretical proposal that reinstated mnemonic information in hippocampus serves as evidence for memory-based decision making (Lisman and Grace, 2005; Norman and O'Reilly, 2003). To this end, we assessed the link between neural reinstatement of specific memory content in MTL subregions, including the hippocampus, and decisions about the memory probes with a mathematical model of decision making commonly used to assess how perceptual evidence impacts decisions (Ratcliff, 1978). Critically,

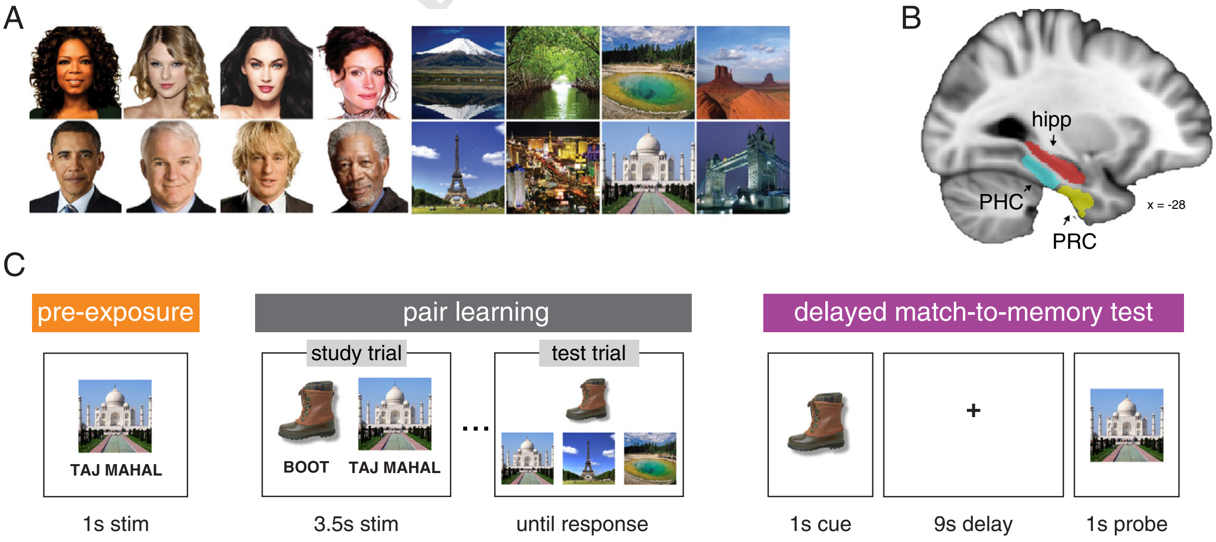

Fig. 1. Schematic of experimental task and depiction of brain regions of interest (ROIs). (A) Eight famous face and eight famous place images were used as stimuli in the experiment. (B) Analyses were conducted in MTL subregions: PHC (light blue), PRC (yellow), and the hippocampus (red). (C) The experiment consisted of three phases. In the pre-exposure phase, participants viewed images of faces, places, objects, and fixation points in isolation. During the pair learning phase, participants learned to criterion eighty paired associates consisting of a common real-world object and either a famous face or place through repetitions of first studying all pairs followed 3AFC tests on associate memory. Finally, participants were tested on each of the eighty pairs during a delayed match-to-memory (DMTM) test. Each test trial consisted of: an object cue (1 s), a delay period (9 s), a probe face or place (1 s) followed by an inter-trial interval (5-11 s, mean 7.5 s). The probe item was either the correct paired associate (a match) or a same-category foil drawn from another pair (a mismatch). Participants indicated match or mismatch status with a button response.

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