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Research report

The retrieval of perceptual memory details depends on right hippocampal integrity and activation

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ABSTRACT

We assessed whether perceptual richness, a defining feature of episodic memory, depends on the engagement and integrity of the hippocampus during episodic memory retrieval. We tested participants' memory for complex laboratory events (LEs) that differed in perceptual content: short stories were either presented as perceptually rich film clips or as perceptually impoverished narratives. Participants underwent functional magnetic resonance imaging (*f*MRI) while retrieving these LEs (narratives and clips), as well as events from their personal life (autobiographical memories). In a group of healthy adults, a conjunction analysis showed that both real-life and laboratory memories engaged overlapping regions from an autobiographical memory (AM) retrieval network, indicating that laboratory memories mimicked autobiographical events successfully. A direct contrast between the film clip and the narrative laboratory conditions identified regions activated by the retrieval of perceptual memory content, which included the right hippocampus, parahippocampal gyrus, middle occipital gyrus and precuneus. In individuals with medial temporal lobe epilepsy (mTLE) originating from the right hippocampus, the magnitude of this "perceptually rich" signal was reduced significantly, which is consistent with evidence of reduced perceptual memory content in this clinical population. In healthy controls, right hippocampal activation also correlated positively with a behavioral measure of perceptual content in the clip condition. Thus, right hippocampal activity contributed to the retrieval of perceptual episodic memory content in the healthy brain, while right hippocampal damage disrupted activation in regions that process perceptual memory content. Our results suggest that the hippocampus contributes to recollection by retrieving and integrating perceptual details into vivid memory constructs.

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1. Introduction

It is well established that the human hippocampus plays an essential role in recollection, the sense of traveling mentally back in time to relive past events (e.g., Moscovitch & McAndrews, 2002; Moscovitch et al., 2005; Nadel & Moscovitch, 1997; Piolino, Desgranges, & Eustache, 2009; Ranganath, 2010; Rugg & Vilberg, 2013). The nature of the cognitive processes and neural mechanisms through which hippocampal activity gives rise to an evocative memory experience, however, is under debate. With the current study, we investigated whether hippocampal activation and integrity are essential to the retrieval of rich sensory-based memory details. Our goal was to advance our understanding of hippocampal function by documenting a mechanism bridging hippocampal activation to the phenomenological experience of recollection.

Most current theories of hippocampal function stipulate that this structure is essential for episodic memory to retain its signature context-specific details (Tulving, 1985, 2002). Multiple Trace Theory (Moscovitch et al., 2005; Nadel & Moscovitch, 1997) and, more recently, the Transformation Hypothesis of memory consolidation (Winocur & Moscovitch, 2011; Winocur, Moscovitch, & Bontempi, 2010), both suggest that most memory loses contextual specificity over time, but that memories that retain their specificity and level of detail remain dependent on the hippocampus. According to the Binding of Items and Contexts model (Diana, Yonelinas, & Ranganath, 2007; Ranganath, 2010), the hippocampus supports memory representations that integrate elements into their context, and memory episodes are an example of such integrated representations. Building on this model, Yonelinas (2013) has suggested that the hippocampus performs *complex high-resolution binding* of the different qualitative aspects of an event, both at encoding and at retrieval. Others have proposed that the hippocampus's main role is to integrate disparate elements into complex spatial scenes (Hassabis & Maguire, 2007; Hassabis, Kumaran, & Maguire, 2007) or simulations of future events (Addis, Cheng, & Schacter, 2011; Schacter, Addis, & Buckner, 2007). While these theories consider hippocampal function differently, each of them predicts that the hippocampus is essential to retrieve highly context-specific details that comprise our memories for past episodes.

In this theoretical context, we hypothesized that retrieval of sensory-based episodic memory details, or perceptual details, is particularly likely to depend on the hippocampus. Perceptual richness is a core feature of episodic memory that contributes to how vividly we re-experience past life events (Brewer, 1986, 1995; Conway, 2009; Rubin, Schrauf, & Greenberg, 2003). During recall, visual elements are combined into "scenes" that form the spatial context in which memories are staged. Moreover, perceptual memory details are highly context-specific: percepts do not easily become generalized or abstract, and therefore they form the core of *high-resolution* content (Yonelinas, 2013). Although some perceptual elements can become integrated into a storyline (e.g., Monica Lewinski's blue dress), most of the sights, sounds, smells and other percepts that render memory vivid are peripheral to an event's main themes. In other words, they are unlikely to become part of a memory's gist which, according to Winocur and Moscovitch (Winocur & Moscovitch, 2011; Winocur et al., 2010), can be retained and accessed without involving the hippocampus. For these reasons, we propose that perceptual memory content is a sensitive marker of recollection, and that it should be an important determinant of hippocampal engagement during memory retrieval.

Although some evidence exists in the literature linking hippocampal function to the retrieval of perceptual memory details, this evidence suffers from important limitations. Perceptual richness emerges from the integration of sensory-based memory details into multidimensional memories. However, the study of rich and complex memories—i.e., autobiographical memory (AM)—offers limited experimental control. For example, emotional content and personal significance are memory characteristics that both correlate with perceptual content (Daselaar et al., 2008; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Rubin et al., 2003) and that are known to modulate hippocampal activity at recall (Addis, Moscovitch, Crawley, & McAndrews, 2004). On the other hand, most tasks of episodic memory conducted in the laboratory (e.g., item recognition or source memory tasks) make use of stimuli too elemental to capture perceptual richness because this feature emerges from complexity. As such, perceptual richness is not typically assessed in a well-controlled laboratory setting, although several recent functional magnetic resonance imaging (*f*MRI) studies using more complex multi-sensory stimuli (e.g., short film clips, Ben-Yakov, Rubinson, & Dudai, 2014; Furman, Mendelsohn, & Dudai, 2012) have shown reliable coding of other event attributes in the hippocampus (Bonnici, Chadwick, et al., 2013; Chadwick, Hassabis, Weiskopf, & Maguire, 2010; Rugg et al., 2012). Nevertheless, some evidence from the literature suggests a link between hippocampal function and memory's perceptual richness. When events are recalled or imagined, hippocampal engagement correlates with ratings of vividness (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Sheldon & Levine, 2013), imagery content (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Viard et al., 2007) and sense of reliving (St Jacques, Kragel & Rubin, 2011; Viard, Desgranges, Eustache, & Piolino, 2012; but see Daselaar et al., 2008). Damage to the medial temporal lobe (MTL) also leads to a deficit in scene construction (Hassabis, Kumaran, Vann, & Maguire, 2007; Hassabis & Maguire, 2007, 2009) and to a paucity of perceptual AM features (St-Laurent, Moscovitch, Jadd, & McAndrews, 2014; St-Laurent, Moscovitch, Levine, & McAndrews, 2009).

With the current study, we performed a direct test of the relationship between episodic memory's perceptual richness and hippocampal function. We tested healthy controls and individuals with unilateral medial temporal lobe epilepsy (mTLE), a condition that compromises the integrity of the MTL including the hippocampus proper, on a memory task while they underwent *f*MRI. The task, which was adapted from a behavioral paradigm we introduced (St-Laurent et al., 2014), was designed to capture the complexity of AM while