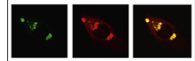


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Research Report

Neural reinstatement and the amount of information recollected



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ARTICLE INFO

Article history:

Accepted 16 July 2014

Available online 24 July 2014

Keywords:

fMRI

Episodic memory

Reinstatement

Recollection

MVPA

Pattern classification

ABSTRACT

Recent functional neuroimaging studies have attempted to understand the cognitive and neural bases of episodic memory retrieval, as well as the extent to which different retrieval judgments reflect qualitative as opposed to continuous changes in neural signals. The present study addressed this issue by investigating the reinstatement of episodic content according to the amount of information available at retrieval. Subjects encoded a series of words in the context of three distinct tasks, while a manipulation of presentation duration (4 or 8 s) was also employed. A later recognition memory test was used to segregate trials according to whether or not they were accompanied by the recollection of details from encoding. Functional MRI data acquired during both the encoding and retrieval phases were used in conjunction with multi-voxel pattern-analysis (MVPA) to provide a measure of the degree to which encoding-related patterns of brain activity were later reactivated (reinstated) at the time of retrieval. Critically, the magnitude of reinstatement differed with respect to the encoding manipulation, such that reinstatement was stronger for items associated with the longer presentation duration. Together with duration-related differences in retrieval activity in left posterior parietal cortex, the results provide neural evidence for the reinstatement of different amounts of episodic information, consistent with the idea that recollection is based on a continuous neural signal.

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1. Introduction

The retrieval of information from episodic memory – often referred to as *recollection* – has been investigated in numerous studies employing behavioral methods, electrophysiology, and functional magnetic resonance imaging (fMRI; for reviews, see [Friedman and Johnson, 2000](#); [Yonelinas, 2002](#); [Wagner et al., 2005](#); [Diana et al., 2007](#); [Rugg and Curran, 2007](#); [Vilberg and Rugg, 2008](#)). Whereas recollection indicates the process by which qualitative details associated with an

episode are consciously retrieved, simple memory judgments (i.e. old/new recognition) can also be supported merely by an acontextual feeling of prior exposure, typically referred to as *familiarity*. Despite continued debate over the degree to which these two processes are dissociable on the basis of behavioral data alone ([Wixted, 2007](#); [Yonelinas and Parks, 2007](#)), consistent sets of brain regions appear to be selectively sensitive to each process. Recollection has been associated with a network of regions including the hippocampus, parahippocampal cortex, medial prefrontal cortex, ventrolateral parietal

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cortex, and posterior cingulate/retrosplenial cortex (for recent meta-analyses, see [Spaniol et al., 2009](#); [Kim, 2010](#)). By comparison, familiarity-based recognition judgments have been correlated with activity in perirhinal cortex, dorsolateral parietal cortex, precuneus, and lateral and anterior prefrontal cortex ([Yonelinas et al., 2005](#); [Montaldi et al., 2006](#); also see [Kim, 2010](#)).

Building upon evidence that the neural correlates of recollection can, to some extent, be isolated, several recent fMRI studies have attempted to further elucidate the functional roles of these recollection-sensitive regions. One such role garnering considerable attention is based on the finding that activity in these regions varies according to the amount of episodic information retrieved. While some of these studies have asked subjects to explicitly report the number of details they recollect about rich study episodes ([Vilberg and Rugg, 2007, 2009b](#)), others have employed encoding manipulations such as presentation duration ([Vilberg and Rugg, 2009a](#)) and repetition ([Guerin and Miller, 2011](#)), which presumably allow for additional information to be encoded over the extended time periods. For example, [Vilberg and Rugg \(2009a\)](#) had subjects encode events comprised of multiple pictures for either one or six seconds. A later recognition memory test involved presentation of a single picture at a time while subjects made judgments according to the standard *remember/know* procedure (hereafter, *R/K*; [Tulving, 1985](#)), allowing trials to be segregated according to whether or not they were accompanied by remembering (recollecting) specific details. [Vilberg and Rugg \(2009a\)](#) observed the typical recollection effect in left posterior parietal cortex (in the vicinity of angular gyrus), whereby activity was elevated for *R* compared to *K* judgments. Moreover, a posterior region within this recollection-sensitive cluster (near the border of Brodmann areas 39 and 19) further differentiated the duration with which items were presented during encoding, such that activity elicited by recollected items was greater when they came from the 6-s condition as opposed to the 1-s condition. An additional memory test following the *R/K* test confirmed that subjects could indeed report more details – such as the accompanying pictures from encoding – about items from the longer duration condition. Together, these results suggest that presentation duration at encoding makes available different amounts of information associated with episodes, and that posterior parietal cortex is sensitive to these graded changes in the amount of information recollected (also see [Vilberg and Rugg, 2007, 2009b](#); [Guerin and Miller, 2011](#)).

The findings described above are consistent with recollection being based on a continuous neural process or signal, as has been recently proposed elsewhere ([Wixted, 2007](#); [Mickes et al., 2009](#); [Wixted and Mickes, 2010](#)). However, evidence for amount-sensitive recollection-related activity in posterior parietal cortex is largely indirect to this hypothesis, given that there is considerable uncertainty and disagreement about the functional role of this region in retrieval (see [Wagner et al., 2005](#); [Vilberg and Rugg, 2008](#); [Hutchison et al., 2009](#); [Shimamura, 2011](#); [Cabeza et al., 2012](#)). On one hand, it has been suggested that this region serves as a buffer for accumulating or actively maintaining retrieved information in service of making a retrieval decision ([Vilberg and Rugg,](#)

[2008, 2009a](#); [Yu et al., 2012](#)). On the other hand, the same effects have also been interpreted as reflecting the bottom-up capture of attention by information retrieved from memory ([Cabeza et al., 2008](#); [Ciaramelli et al., 2008](#)). In the [Vilberg and Rugg \(2009a\)](#) study, the behavioral measures indicating that different amounts of information were recollected came from an experimental phase separate from that in which fMRI data were acquired, making it unclear whether different amounts of information were actually retrieved during the *R/K* test. One way this issue can potentially be addressed is by requiring subjects to indicate with overt responses the amount retrieved ([Vilberg and Rugg, 2007, 2009b](#)). However, this procedure could elicit other, confounding effects such as encouraging subjects to strategically focus on this information, or to engage to different degrees in post-retrieval processing (also see [Vilberg and Rugg, 2009a](#)) – neither of which addresses the recovery (recollection) of information. An alternative strategy is to employ a measure of episodic information that can be tracked during the retrieval phase, orthogonal to any behavioral response(s) being made. The advantage of this approach is that no reference to the information needs to be made during the retrieval phase, minimizing the use of any strategies focused on that information. The present study adopts this strategy by using a neural measure of episodic content.

To begin to address how episodic information from encoding can be used to understand the basis of retrieval, we must first consider the brain processes typically thought to give rise to recollection. According to several neurally-inspired computational models, episodic retrieval involves re-engaging the cognitive and neural representations and processes that were engaged when an event was encoded ([Alvarez and Squire, 1994](#); [McClelland et al., 1995](#); [Hasselmo and Wyble, 1997](#); [Rolls, 2000](#); [Shastri, 2002](#); for further discussion, see [Rugg et al., 2008](#)). A key assumption of this account is that events elicit distributed patterns of cortical activity at the time of encoding, due to the spatiotemporal characteristics associated with the events as well as the cognitive operations and representations activated through elaborative processing. The hippocampus indexes these cortical patterns, which can be largely overlapping from event to event, by assigning them distinct (sparse) representations ([Marr, 1971](#); [Teyler and DiScenna, 1986](#); [Norman and O'Reilly, 2003](#)). When a retrieval cue for the event is subsequently encountered, the cue activates a portion of the original cortical activity, which in turn engages the corresponding hippocampal representation. Finally, the hippocampal representation reinstates the complete pattern of cortical activity, allowing for the recollection of other details (i.e. those not provided by the retrieval cue) that were associated with the original event ([Norman and O'Reilly, 2003](#)).

Operating under the framework described above, several studies have employed fMRI to investigate the involvement of reinstatement during episodic retrieval (for reviews, see [Rugg et al., 2008](#); [Danker and Anderson, 2010](#); [Rissman and Wagner, 2012](#)). These studies typically adopt a behavioral design in which items from multiple classes (e.g., from different modalities or having different task requirements) are presented at encoding, with the goal to elicit distinct patterns of cortical activity between classes. On a later

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