



Episodic retrieval involves early and sustained effects of reactivating information from encoding

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ARTICLE INFO

Article history:

Accepted 9 November 2014

Available online 15 November 2014

Keywords:

Episodic memory
Recognition
EEG
Reinstatement
Reactivation
Confidence

ABSTRACT

Several fMRI studies have shown a correspondence between the brain regions activated during encoding and retrieval, consistent with the view that memory retrieval involves hippocampally-mediated reinstatement of cortical activity. With the limited temporal resolution of fMRI, the precise timing of such reactivation is unclear, calling into question the functional significance of these effects. Whereas reactivation influencing retrieval should emerge with neural correlates of retrieval success, that signifying post-retrieval monitoring would trail retrieval. The present study employed EEG to provide a temporal landmark of retrieval success from which we could investigate the sub-trial time course of reactivation. Pattern-classification analyses revealed that early-onsetting reactivation differentiated the outcome of recognition-memory judgments and was associated with individual differences in behavioral accuracy, while reactivation was also evident in a sustained form later in the trial. The EEG findings suggest that, whereas prior fMRI findings could be interpreted as reflecting the contribution of reinstatement to retrieval success, they could also indicate the maintenance of episodic information in service of post-retrieval evaluation.

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Introduction

Successful memory retrieval is thought to depend on the degree to which processes engaged during encoding of the memory are re-engaged upon presentation of a retrieval cue (Bower, 1972; Damasio, 1989). This principle is reflected by a common experience in daily life, when difficulty recalling a memory is sometimes resolved by retracing the activities leading up to the initial experience. In experimental psychology, studies providing initial evidence for this idea demonstrated improvements in memory performance as a result of having subjects re-engage encoding-related cognitive processes during a memory test (Tulving and Thomson, 1973; Morris et al., 1977). Further support for the idea comes from highly-influential neurobiological models that have guided episodic memory research for the past 20 years (Alvarez and Squire, 1994; McClelland et al., 1995; Rolls, 2000). A fundamental feature of these models, with respect to the conscious retrieval (“recollection”) of episodic information, is the involvement of the hippocampus. During encoding, cortical activity patterns elicited by an event are represented rapidly and sparsely by the hippocampus (Marr, 1971; Teyler and DiScenna, 1986; Shastri, 2002). Upon retrieval cue presentation, the hippocampal representation is reactivated, thereby reinstating the cortical pattern that was present during encoding and allowing for the recollection of additional episodic information

(i.e. not inherent in a partial cue; Hasselmo and Wyble, 1997; Norman and O'Reilly, 2003).

Functional magnetic resonance imaging (fMRI) studies have been instrumental in providing empirical evidence of neural reinstatement during episodic retrieval (for reviews, see Rugg et al., 2008; Danker and Anderson, 2010). These studies test the simple prediction that the pattern of brain activity at encoding should match that at retrieval. In an early study, Wheeler et al. (2000) had subjects encode words paired with either a picture or an auditory stimulus. An important feature of their design, carried forth to subsequent studies and the present one, was that the cues presented during a later memory test were perceptually uninformative about the previous encoding condition in which they appeared. Thus, any brain activity specific to a previous encoding condition was inferred to have resulted from retrieving the associated picture or auditory information. Wheeler et al. demonstrated that cues from each condition during retrieval reactivated a subset of the regions active at encoding (also see Kahn et al., 2004; Johnson and Rugg, 2007). More recently, multivariate pattern analysis (MVPA; see Haynes and Rees, 2006; Norman et al., 2006; Tong and Pratte, 2012) of fMRI data has been used to investigate reinstatement by training a pattern classifier to distinguish brain activity associated with different conditions at encoding and then independently evaluating that classifier on data from a memory test (for review, see Rissman and Wagner, 2012). The classifier's ability to identify an item's encoding history depends on the encoding-retrieval similarity of neural patterns, thus providing an index of reinstatement. In one study, Johnson et al. (2009) used MVPA to assess reinstatement across two subjectively-

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different retrieval experiences — an acontextual sense of familiarity and the recollection of specific details from encoding (Yonelinas, 2002). The magnitude of pattern reactivation increased in a graded manner across these experiences, suggesting that they are supported by changes in a common neural process. Together with other results based on this analysis strategy (e.g., Polyn et al., 2005; McDuff et al., 2009; Kuhl et al., 2011, 2012; Staresina et al., 2012), these findings demonstrate the utility of tracking reactivation across different memory judgments to further understand the role(s) of reinstatement in retrieval.

Whereas the fMRI studies described above have convincingly demonstrated the involvement of encoding-related reactivation during retrieval, the fact that they rely on the relatively slow hemodynamic response is a limiting factor in assessing the timing of reinstatement effects. One notable exception is the study by Polyn et al. (2005), which temporally isolated reactivation occurring before a retrieved item was reported; however, given that those effects likely reflect preparatory (or categorical) rather than item-specific processing, the sub-trial timing of neural events related to retrieval success are yet to be determined. In keeping with the models described earlier, hippocampally-mediated reinstatement is thought to allow episodic information to become available for conscious retrieval (Norman and O'Reilly, 2003; Norman, 2010). Implicit in this assertion is the assumption that reactivation effects should precede, or at least coincide with, the neural correlates of retrieval success. The findings of episodic retrieval studies employing neural measures with high temporal resolution, such as electroencephalography (EEG), are relevant to this issue. These studies have consistently identified a retrieval success correlate over the left posterior scalp that onsets within about 500 ms following cue presentation (Friedman and Johnson, 2000; Rugg and Curran, 2007). This EEG correlate has additionally been associated with subjective aspects of retrieval, as evidenced by its enhancement when subjects consciously recollect details or are highly confident about retrieval (Wilding and Rugg, 1996; Düzel et al., 1997; Curran, 2004). The effect thus serves as a landmark from which other retrieval-supporting processes, having distinct scalp topographies and time courses, can be dissociated. According to this framework, neural processes or events that contribute to retrieval success must occur quickly enough upon cue presentation so as to inform other neural events and, ultimately, the behavioral response. Alternatively, the timing of reactivation might follow retrieval success effects, such as is the case with neural correlates of post-retrieval processing (e.g., Wilding and Rugg, 1996; Hayama et al., 2008). In this latter case, reinstatement would be considered to reflect the maintenance of retrieved information in service of evaluative processes that vary with retrieval demands (Koriat and Goldsmith, 1996).

Recent studies have begun to investigate the sub-trial timing of retrieval-related reactivation with EEG (Wimber et al., 2012) and magnetoencephalography (MEG; Jafarpour et al., 2014) in order to overcome the relatively poor temporal resolution of fMRI. In one study, Jafarpour et al. (2014) employed MEG data and MVPA to investigate the reinstatement of neural activity that occurred early during a given encoding trial. Subjects studied words paired with scene or face stimuli, and then undertook a memory test in which they distinguished judgments associated with recollection from those based on high-confidence familiarity (with a variant of the “remember/know” task; Tulving, 1985). An early MEG component discriminating between the scenes and faces was identified at 180 ms after encoding stimulus onset. This component was then shown to be reactivated by around 500 ms after the onset of word retrieval cues that were designated with remember judgments. These effects are thus in the appropriate time window for contributing to retrieval success. However, Jafarpour et al. (2014) note that they had insufficient numbers of trials to test for reactivation associated with other retrieval judgments. As a result, it is unclear whether reactivation varied across judgments, as would be expected if it played a role in retrieval outcome (Kahn et al., 2004; Johnson and Rugg, 2007; Johnson et al., 2009). A similar critique can

be made regarding the results of the study by Wimber et al. (2012). Wimber et al. (2012) had subjects encode words in the context of flickering visual stimuli (6 and 10 Hz) and later make confidence judgments about the words. Whereas some aspects of the frequency information in the EEG data (orientation for 6 Hz and variance for 10 Hz) indicated greater reactivation during high-confidence judgments compared to misses, a secondary behavioral experiment showed that subjects were at chance in identifying the flicker associated with test items. These findings therefore raise the possibility that the reactivation signifies some implicit availability (i.e. priming) of encoding content rather than being functionally related to conscious retrieval. In the current study, we address this issue by employing encoding conditions that have previously been shown to elicit accurate source-memory judgments (McDuff et al., 2009).

The enhanced temporal resolution of reactivation effects described above brings with it another issue about timing that must also be addressed. Although identifying the sub-trial time course of reactivation during retrieval is important (as in Wimber et al., 2012; Jafarpour et al., 2014), the detection of such effects could also be limited by variability (mismatch) in the timing of activated patterns going from encoding to retrieval. For example, a pattern activated late during an item's encoding episode could be activated relatively early during the corresponding retrieval of that item; likewise, the order in which patterns are activated may also differ between the two phases. Systematic examples of this timing mismatch can be found in animal studies in which the reactivation of hippocampal neural firing sometimes occurs more rapidly, and even in the reverse order, compared to that during learning (Lee and Wilson, 2002; Foster and Wilson, 2006). Jafarpour et al. (2014) accounted for such variability, in part, by focusing on a neural pattern at a specific time during encoding and then testing for the reactivation of that pattern throughout the retrieval trial. However, it is reasonable to assume that representations and processes engaged at different time points of an encoding trial could also potentially be reactivated during retrieval of that item. Indeed, encoding tasks are typically structured to allow for this sort of elaborative processing by providing subjects with ample time (multiple seconds) on each item. There is a need therefore to not only track information across successive retrieval time points, but also maximize the accumulation of encoding-related information at each of those points. We accomplish this in the current study with a procedure recently used by Fuentesmilla et al. (2010). In that study, pattern classifiers were trained on MEG data from an encoding period (3 s) but then tested on data from a longer period of working-memory maintenance (5 s). The key feature of this procedure is in tracking the *number* of reactivations during maintenance, as opposed to reactivation strength (cf. Johnson et al., 2009), allowing for timing disparities between the training and testing data (for similar application to longer, resting periods, see Staresina et al., 2013). Here, we extend this procedure to the sub-trial time courses of different processes involved in episodic retrieval, as identified using EEG.

The current study investigated the involvement of reactivation effects that are considered early and late, with respect to neural correlates of retrieval success, during episodic retrieval. Subjects completed an encoding phase in which they were presented with a series of words in the context of three tasks, designed to elicit distinct neural activity patterns. The *Artist* task involved thinking about how an artist would draw the item denoted by the word, the *Function* task instructed subjects to generate different functions for the item, and the *Cost* task directed subjects to think about the item's relative cost (cf. Johnson et al., 2009; McDuff et al., 2009). The use of different tasks for the encoding manipulation also allowed us to address whether early reactivation was restricted to stimulus-related (sensory) information from encoding (e.g., the visual flicker in Wimber et al., 2012; the faces and scenes in Jafarpour et al., 2014) or could be extended to the domain of task-related cognitive operations that are largely generated by subjects (e.g., given the Function cue, a number of possible functions

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