NeuroImage 172 (2018) 228–238

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Direct electrophysiological evidence for the maintenance of retrieval orientations and the role of cognitive control

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ARTICLE INFO

Keywords:
Retrieval orientation
Episodic memory
Cognitive control
Post-retrieval processing
Event-related potential
Electrophysiology

ABSTRACT

Retrieval orientations are memory states that bias retrieval towards specific memory contents. Many neuroimaging studies have examined the influence of retrieval orientations on stimulus processing, but very little direct evidence exists regarding the ongoing maintenance of orientations themselves. Participants completed two memory tasks with different retrieval goals. ERPs were time-locked to a pre-stimulus fixation asterisk and contrasted according to retrieval goals. Pre-stimulus ERPs elicited during the two retrieval tasks diverged at frontal electrode sites. These differences onset early and were sustained throughout the fixation-stimulus interval. The functional and spatiotemporal characteristics of this ERP effect comprise the first direct electrophysiological evidence of the ongoing maintenance of retrieval orientations throughout a task. Moreover, this effect was eliminated in participants who performed a stroop task prior to the memory tests, indicating that reserves of cognitive control play an important role in the maintenance of retrieval orientations throughout memory tasks.

Introduction

Our episodic memories create the record of our lives, forming a vast library of past experiences rich in sensory, social, emotional and cognitive detail. Researchers are increasingly interested in the ways in which we edit and navigate our memories, searching for desired memories while inhibiting the retrieval of unwanted or irrelevant information. There is now considerable evidence from event-related potential (ERP) and functional MRI studies that cognitive processing during intentional memory retrieval can be oriented towards specific task-relevant features of prior episodes via the adoption of task-specific memory states called 'retrieval orientations' (Johnson et al., 1997; Ranganath and Paller, 1999; Rugg et al., 2000; Robb and Rugg, 2002; Herron and Rugg, 2003; Dzulkifli et al., 2004; Herron and Wilding, 2004; Hornberger et al., 2004, 2006a; Werkle-Bergner et al., 2005, b; Stenberg et al., 2006; Woodruff et al., 2006; Benoit et al., 2009; Bridger et al., 2009; McDuff et al., 2009; Bridger and Mecklinger, 2012; Halsband et al., 2012; Morcom and Rugg, 2012; Rosburg et al., 2013, 2014; Roberts et al., 2014; Johnson and McGhee, 2015; Gao et al., 2016; Herron et al., 2016). It is believed that these memory states are maintained for the duration of the requirement to retrieve specific types of contextual information from a prior episode, and that they influence the ways in which incoming stimuli are processed (Rugg and Wilding, 2000).

Neural correlates of retrieval orientations are typically obtained by intermixing previously studied and new items in recognition memory tests, and varying the contextual retrieval requirements throughout these test/s. Retrieval orientations are thought to exert a top-down influence on retrieval stimulus processing to facilitate the retrieval of goal-relevant contextual information (Rugg and Wilding, 2000). This hypothesis predicts that identical retrieval stimuli will be processed differently according to the type of contextual details that participants are attempting to retrieve from the encoding episode. Many studies of retrieval orientation have therefore contrasted neural activity elicited by new items associated with different retrieval demands, as these items should be sensitive to the top-down influence of different retrieval orientations without confounding these with differences in retrieved content. The majority of these studies have obtained neural correlates of retrieval orientation by employing paradigms in which different retrieval demands were imposed in different testing blocks, with the precise spatiotemporal characteristics of the correlates of orientation varying across studies depending on the tasks employed as would be expected of a context-specific effect. Until recently, it appeared that while orientation-related neural differences in retrieval stimulus processing were evident in blocked designs, they were not evident when different retrieval demands were intermixed within the same memory test (Wilding and Nobre, 1999; Werkle-Bergner et al., 2005; Herron and Wilding, 2006; Johnson and Rugg, 2006; Benoit et al., 2009). However, we recently demonstrated that it is possible for participants to flexibly

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https://doi.org/10.1016/j.neuroimage.2018.01.062
Received 11 October 2017; Received in revised form 11 January 2018; Accepted 24 January 2018

adjust retrieval cue processing in accordance with rapidly changing retrieval orientations if a combination of directed preparatory cues and highly differentiated retrieval tasks are employed (Herron et al., 2016). The cognitive operations reflected by stimulus-locked correlates of retrieval orientation appear to play an important role in memory retrieval, as it has been demonstrated that the magnitude of these correlates are positively correlated with retrieval accuracy in individual differences analyses (Bridger et al., 2009; Rosburg et al., 2011, 2014; Bridger and Mecklinger, 2012; Sprondel et al., 2013).

Taking a somewhat different approach, a series of ERP studies from our laboratory capitalised upon the high temporal resolution of the technique by presenting pre-stimulus preparatory cues that directed participants to prepare to retrieve different kinds of contextual information (encoding task or spatial location) upon presentation of the retrieval stimulus (Herron and Wilding, 2004, 2006; Herron et al., 2016). Each preparatory cue type was presented for at least two consecutive trials before switching to a different cue type. Sustained preparatory differences were observed during the cue-stimulus interval according to the retrieval requirements indicated by the cue in all three studies, but the nature of these effects varied with experimental parameters. When participants were required to switch between two source memory tasks, preparatory indices of retrieval orientation were apparent only on the first trial of a particular cue-type (‘switch’ trials) between 700 and 1900ms post-cue at left anterior sites, being absent on the subsequent ‘stay’ trial, and also absent when the two tasks were predominantly blocked (Herron and Wilding, 2006). This functional property suggests that this preparatory correlate of retrieval orientation is related to processes involved in the initial adoption of a retrieval orientation (such as task set configuration), but which are not important for the maintenance of the retrieval state once established (Herron and Wilding, 2006). This preparatory correlate of retrieval orientation was also evident in our earlier study (Herron and Wilding, 2004), but did not onset until the stay trial. As this study also included a third non-episodic task, we proposed that this additional cognitive load may have delayed adoption of the appropriate orientation.

This sustained ERP modulation was replaced by an earlier effect of retrieval cue-type on both switch and stay trials in our most recent study (Herron et al., 2016). This experiment used single non-counterbalanced word questions (e.g. ‘left?’ ‘animacy?’) as preparatory cues that required simple yes/no responses according to whether the stimulus was associated with the source specified by the cue. These retrieval requirements derive from the exclusion task (Jacoby, 1991) in which a ‘target’ source is designated by the experimenter and participants make positive recognition judgments only to items from that source. This is in contrast to the two earlier studies which had used more abstract letters or symbols as cues, and which also required more complex three-way source judgments (e.g. left/right/new). It may therefore be the case that these more constrained and targeted cues allowed retrieval orientations to be initiated more rapidly (Herron et al., 2016). However, it is also possible that these early effects simply reflect perceptual differences between cue-types, an interpretation supported by the fact that this effect was also evident when letters were consistently assigned to cue-types (Herron and Wilding, 2004) but not when counterbalanced symbols were used as cues (Herron and Wilding, 2006). A third potentially explanatory factor is that the two studies in which this earlier effect was observed also included a third task; a semantic task in Herron and Wilding (2004), and a recognition task in Herron et al. (2016). It therefore remains to be seen whether early effects of cue-type are still observed under more constrained retrieval requirements when both visual differences between cue-types and the requirement to switch in/out of a third non-source memory task are removed from the design.

Despite the conceptualisation of retrieval orientations as sustained memory states, direct electrophysiological correlates of their maintenance throughout tasks have proven elusive to date. As described above, ERP correlates of retrieval orientation obtained thus far have been related to i) the initial adoption of an orientation, and ii) the downstream task-dependent processing of stimuli, but direct correlates of the maintenance of the orientation itself have been technically challenging to obtain. Similarly, fMRI studies have reported retrieval orientation effects contingent upon the processing of new items (Hornberger et al., 2006a; Morcom and Rugg, 2012) as well as stimulus-locked effects of retrieval task that are insensitive to retrieval success (Dobbins et al., 2003). Woodruff et al. (2006) reported fMRI data supporting the existence of state-related retrieval orientations by employing a mixed design in which stimulus-related effects were modelled and separated from sustained neural activity that varied in accordance with retrieval goals. The high temporal resolution of ERPs allows for a pre-stimulus time window in which more direct measures of brain activity linked to sustained retrieval orientations can potentially be observed without contamination by stimulus-related effects. Analysis of ERPs recorded during this pre-stimulus window has thus far been restricted to paradigms in which participants switch between different retrieval tasks, but utilising this window in conjunction with blocked retrieval requirements may provide insights into neural activity linked to the maintenance of retrieval orientations.

Retrieval orientations have been linked to the cognitive control of episodic retrieval via the presence of stimulus-locked orientation effects in conjunction with neural evidence of ‘strategic retrieval’ (Herron and Rugg, 2003; Dzulkifli and Wilding, 2005; Dzulkiflil et al., 2006; Morcom and Rugg, 2012; Rosburg et al., 2013; Mao et al., 2017). Strategic retrieval refers to the controlled recollection of task-relevant contextual details alongside a reduction in the recollection of less-relevant memories. Many studies of strategic retrieval borrow from the aforementioned ‘exclusion’ paradigm (Jacoby, 1991), in which items are encoded in at least two different encoding contexts (e.g. two different encoding tasks) and then intermixed with new items in an exclusion memory test. Participants are required to endorse items from a designated encoding context on one response key (‘targets’) and to reject items from the alternate encoding context (‘nontargets’) on the same response key as new items. Neural evidence for strategic retrieval takes the form of significantly larger neural correlates of recollection for targets than for nontargets, these being the ‘left parietal old/new effect’ in ERP studies (i.e. a positive-going shift at left parietal electrode sites for recollected items; (Herron and Rugg, 2003; Dzulkifli and Wilding, 2005; Rosburg et al., 2013; Mao et al., 2017)) and left angular gyrus activation in the fMRI parallel (Morcom and Rugg, 2012). The fact that all of these studies reported neural correlates of strategic retrieval in conjunction with stimulus-locked neural correlates of retrieval orientation indicates that strategic retrieval may be enabled by the maintenance of target-centric retrieval orientations which facilitate the recollection of target memories at the expense of nontarget memories.

Two ERP studies examined the role of cognitive control and working memory capacity (WMC) during strategic retrieval (Elward and Wilding, 2010; Elward et al., 2013). The first study (2010) showed that individual measures of WMC (measured using O-span performance) were positively correlated with ERP indices of recollection and strategic retrieval; the magnitude of the target left parietal effect increased with WMC, and the degree to which the target left parietal effect was larger than the nontarget left parietal effect was also positively correlated with WMC. In a second study (2013), individuals with high WMC who completed a stroop task prior to the memory test exhibited no ERP evidence of strategic retrieval, whereas these were apparent following a control task. The stroop task (Stroop, 1935) requires participants to name the color of the ink in which color names are printed. The two are predominantly incongruous, which means that cognitive control is required to overcome this interference. Because cognitive control is a finite resource, research has shown that taxing these reserves can impair performance on subsequent tasks requiring cognitive control (also referred to as executive function or self-regulation; Baumeister et al., 1998; Muraven and Baumeister, 2000). It has also been shown that autobiographical memory retrieval can be impaired if a stroop task is completed prior to testing (Neshat-Doost et al., 2008; Dahm et al., 2011). Elward et al.'s (2013)