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Research Report

Preparation breeds success: Brain activity predicts remembering

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ABSTRACT

Successful retrieval of episodic information is thought to involve the adoption of memory states that ensure that stimulus events are treated as episodic memory cues (retrieval mode) and which can bias retrieval toward specific memory contents (retrieval orientation). The neural correlates of these memory states have been identified in many neuroimaging studies, yet critically there is no direct evidence that they facilitate retrieval success. We cued participants before each test item to prepare to complete an episodic (retrieve the encoding task performed on the item at study) or a non-episodic task. Our design allowed us to separate event-related potentials (ERPs) elicited by the preparatory episodic cue according to the accuracy of the subsequent memory judgment. We predicted that a correlate of retrieval orientation should be larger in magnitude preceding correct source judgments than that preceding source errors. This hypothesis was confirmed. Preparatory ERPs at bilateral frontal sites were significantly more positive-going when preceding correct source judgments than when preceding source errors or correct responses in a non-episodic baseline task. Furthermore this effect was not evident prior to recognized items associated with incorrect source judgments. This pattern of results indicates a direct contribution of retrieval orientation to the recovery of task-relevant information and highlights the value of separating preparatory neural activity at retrieval according to subsequent memory accuracy. Moreover, at a more general level this work demonstrates the important role of pre-stimulus processing in ecphory, which has remained largely neglected to date.

1. Introduction

Many of the stimuli that we encounter in everyday life have associations with the past. There are many people who we meet, places that we pass and items that we see or use that would be excellent cues for events from our personal past. For example, when I look at my watch to tell the time I could recover details of the episode when I was given it as a gift. However these memories typically do not come to mind. Given the abundance of cues that we are confronted with it is

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perhaps surprising that we are not constantly reminiscing. What this demonstrates is that having a cue and a relevant past experience does not guarantee the recovery of information. So what else is required? According to Tulving (1983), in order for an individual to remember a particular episode they need to enter a cognitive state where stimulus events are treated as episodic memory cues. Thus another important prerequisite for remembering is that the individual should be in a state of mind that is focused on their personal past, known as retrieval mode.

We know little about retrieval mode. The work that has been conducted in this area has tended to use neuroimaging techniques, due to the difficulty in studying cognitive states using behavioral measures alone. In order to reveal neural indices of retrieval mode, paradigms have been used where participants switch between different classes of tasks, episodic versus non-episodic, as retrieval mode should only be engaged when individuals are required to retrieve episodic information (Rugg & Wilding, 2000). One of the first studies in this area (Duzel et al., 1999) recorded direct current event-related potentials (ERPs) while participants switched between completing separate blocks of a recognition memory task and a semantic judgment task. A cue, which indicated which task the participant should complete, was presented for 2 s prior to the first of four test words. ERPs associated with the episodic retrieval cue were more positive-going compared to the semantic cue, with differences emerging just after the presentation of the task cue and being sustained for the rest of the block. This effect was maximal at a right frontopolar site, which is consistent with findings from hemodynamic studies of retrieval mode where activation in the right prefrontal cortex has been found (Duzel et al., 2001; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Nyberg et al., 1995; Velanova et al., 2003).

More recent studies using ERPs have presented the task cue before each test item and asked participants to switch between completing tasks with different retrieval demands. This gives an interval, of around 2 s, where the participant knows the task they will need to complete on the subsequent test item. During this preparatory period retrieval mode would be anticipated to be engaged, and importantly neural activity is not contaminated by indices of memory retrieval. Several studies have found differences in slow wave activity at frontal scalp locations for cues indicating preparation for an episodic versus a non-episodic task and this pattern of data has been interpreted as the electrophysiological signature of retrieval mode (Evans, Williams, & Wilding, 2015; Herron & Wilding, 2004, 2006a; Morcom & Rugg, 2002; Wilckens, Tremel, Wolk, & Wheeler, 2011). The divergences can onset quite early (e.g. 300 ms; Herron & Wilding, 2004) but commonly start around 800 ms from the onset of the preparatory cue and are sustained until the test item is presented. In the majority of studies, this effect has been observed on the second trial of the episodic task rather than the first. Drawing from the task-switching literature (Monsell, 2003), it has been concluded on the basis of these findings that retrieval mode cannot be successfully initiated until at least one trial of the episodic task has been completed (Herron & Wilding, 2004, 2006a; Morcom & Rugg, 2002), a phenomenon referred to by Duzel et al. (2001) as 'neurocognitive inertia'. More recently, however, Evans et al. (2015) demonstrated that ERP correlates of retrieval mode can in fact be obtained on the first trial of the episodic task if the contents of the episodic and non-episodic tasks are equated (in this instance, remember the test probe's prior location or make perceptual location judgments) and/or the trial sequence is predicable, thus reducing the cognitive load required to switch between tasks.

Whereas retrieval mode is a general episodic memory state initiated whenever episodic retrieval is required and which remains invariant across different retrieval goals, content-specific memory states – termed 'retrieval orientations' – are engaged when there is a requirement to retrieve specific kinds of episodic information (Rugg & Wilding, 2000). Retrieval orientations are thought to influence stimulus processing to facilitate the retrieval of task-relevant information, and a wide variety of ERP and fMRI studies have therefore contrasted stimulus-locked neural activity across memory tasks with varying retrieval goals to obtain their neural correlates (e.g. Hornberger, Rugg, & Henson, 2006a, 2006b; Bridger, Herron, Elward, & Wilding, 2009; Dzulkifli & Wilding, 2005; Herron & Rugg, 2003; Hornberger, Morcom, & Rugg, 2004; Johnson & McGhee, 2015; McDuff, Frankel, & Norman, 2009; Morcom & Rugg, 2012; Rosburg, Johansson, & Mecklinger, 2013; Rosburg, Johansson, Sprondel, & Mecklinger, 2014; Werkle-Bergner, Mecklinger, Kray, Meyer, & Duzel, 2005; Woodruff, Uncapher, & Rugg, 2006). In keeping with its definition, neural correlates of retrieval orientation vary according to specific retrieval goals.

Preparatory correlates of retrieval orientation have also been studied in ERP experiments which cue participants to switch between different episodic memory tasks (Herron & Wilding, 2004, 2006b). Cues directing participants to prepare to retrieve either location-based information or encoding task elicited differential slow–wave activity at left anterior electrode sites during the cue-stimulus interval. Unlike the majority of studies examining mode, this preparatory correlate of retrieval orientation was observed on the first trial of the task when two episodic cue-types were employed (Herron & Wilding, 2006b). An fMRI study which similarly cued participants to retrieve either encoding list or encoding task reported activation in left lateral anterior prefrontal cortex (Simons, Gilbert, Owen, Fletcher, & Burgess, 2005). The observation that this activation peaked 4s prior to recollection and was additionally evident on trials containing no retrieval stimuli led the authors to propose that this region may have given rise to the preparatory ERP effect reported by Herron and Wilding (2004).

While there is now a substantial body of evidence supporting the existence of retrieval mode and orientation, a critical issue that has not yet been resolved is the relationship between the adoption of these memory states and success in recovering episodic information from memory. If they ensure that stimulus events are treated as episodic memory cues then their engagement should lead to enhanced episodic memory. In the case of retrieval mode, its engagement would be predicted to facilitate episodic memory of any kind, benefiting recognition and both noncriterial (i.e. recollection of details that are irrelevant to task demands, Yonelinas & Jacoby, 1996) and criterial recollection. The initiation of retrieval orientations should lead to more selective