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Goal-dependent modulation of declarative memory: Neural correlates of temporal recency decisions and novelty detection

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Abstract

Declarative memory allows an organism to discriminate between previously encountered and novel items, and to place past encounters in time. Numerous imaging studies have investigated the neural processes supporting item recognition, whereas few have examined retrieval of temporal information. In the present study, functional magnetic resonance imaging (fMRI) was conducted while subjects engaged in temporal recency and item novelty decisions. Subjects encountered three-alternative forced-choice retrieval trials, each consisting of two words from a preceding study phase and one novel word, and were instructed to either identify the novel item (Novelty trials) or the more recently presented study item (Recency trials). Relative to correct Novelty decisions, correct Recency decisions elicited greater activation in a network of left-lateralized regions, including frontopolar and dorsolateral prefrontal cortex and intraparietal sulcus. A conjunction analysis revealed that these left-lateralized regions overlapped with those previously observed to be engaged during source recollection versus novelty detection, suggesting that during Recency trials subjects attempted to recollect event details. Consistent with this interpretation, correct Recency decisions activated posterior hippocampus and parahippocampal cortex, whereas incorrect Recency decisions elicited greater anterior cingulate activation. The magnitude of this latter effect positively correlated with activation in right dorsolateral prefrontal cortex. Finally, correct Novelty decisions activated the anterior medial temporal lobe to a greater extent than did correct Recency decisions, suggesting that medial temporal novelty responses are not obligatory but rather can be modulated by the goal-directed allocation of attention. Collectively, these findings advance understanding of how subjects strategically engage frontal and parietal mechanisms in the service of attempting to remember the temporal order of events, and how retrieval goals impact novelty processing within the medial temporal lobe.

Keywords: Recognition memory; Episodic memory; Recollection; Familiarity; Temporal context; Retrieval orientation

1. Introduction

Declarative memory supports remembering *what* items have been encountered, as well as *when* they were experienced. Discrimination between experienced and novel items can be based on recollection—the retrieval of specific contextual details associated with the item's occurrence – or on familiarity – the sense of having encountered the item in the absence of any specific details (Yonelinas, 2002). Paralleling item recognition, it has been argued that recognizing *when* an item was experienced can be based on recollecting details about the temporal context in which the item appeared, or on an assessment of trace-strength or item familiarity (Curran & Friedman, 2003; Hintzman, 2001, 2003, 2005). Although considerable attention has been focused on specifying the neural mechanisms that support recollection- and familiarity-based item recognition (Aggleton & Brown, 1999; Curran, 2000; Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Norman & O'Reilly, 2003; Ranganath et al., 2004; Squire, Stark, & Clark, 2004; Wheeler & Buckner, 2004), relatively less is known about the neural processes supporting retrieval judgments about temporal information. Moreover, the few neuroimaging studies that have sought to delineate the processes supporting temporal recency decisions have yielded conflicting evidence as to whether such decisions depend on the recollection of event details or on assessments of item familiarity, with these differences potentially stemming from different task constraints across studies.

Specifying which prefrontal cortical (PFC) mechanisms are engaged during temporal recency decisions may provide

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leverage on understanding the bases for such judgments. Extensive prior neuroimaging evidence indicates that left lateral PFC regions – most notably frontopolar and dorsolateral cortices – are selectively engaged when subjects attempt to recollect contextual details about an episode, such as the spatial position in which a stimulus appeared (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Rugg, Fletcher, Chua, & Dolan, 1999) or perceptual or conceptual details associated with the item's prior encounter (e.g., Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Wagner, 2005; Nolde, Johnson, & D'Esposito, 1998; Ranganath, Johnson, & D'Esposito, 2000). By contrast, right dorsolateral and ventrolateral PFC are often engaged when subjects attempt to make familiarity-based discriminations between novel and experienced items (Dobbins & Wagner, 2005; Henson, Shallice, & Dolan, 1999; Henson, Rugg, Shallice, & Dolan, 2000; Kensinger, Clarke, & Corkin, 2003). A central question with respect to understanding the bases of temporal recency judgments is: which PFC subregions are engaged during recency decisions relative to item recognition judgments?

Neuropsychological and electrophysiological studies have implicated PFC in temporal-order or temporal-recency decisions, though the specific PFC subregions associated with such judgments are unclear. Neuropsychological studies indicate that damage to lateral PFC impairs temporal-order retrieval to a greater extent than item recognition (Kesner, Hopkins, & Fineman, 1994; Milner, Corsi, & Leonard, 1991; Shimamura, Janowsky, & Squire, 1990); however, these effects often appear to be lateralized by stimulus type rather than type of retrieval decision. Electrophysiologically, while event-related brain potentials (ERPs) at bilateral PFC electrode sites have been observed to be more positive during correct recency retrieval compared with item recognition (Tendolkar & Rugg, 1998) and during contextually-driven recency decisions compared with those that were less driven by contextual retrieval (Curran & Friedman, 2003), it is difficult to discern the neural generators of these effects, and thus it is unclear which specific PFC subregions contribute to such recency decisions.

Initial results from positron emission tomography and fMRI studies, while offering higher spatial resolution than ERP and most patient studies, have yielded conflicting patterns. On the one hand, the results from a few studies suggest a preferential role of right PFC subregions during temporal recency retrieval compared to item recognition (Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Cabeza et al., 1997) and to conceptual source recollection (Dobbins, Rice, Wagner, & Schacter, 2003). These studies used relatively long lists of study items (60–80 items/list), which may have increased the probability that performance on temporal Recency trials was differentially dependent on familiarity. By contrast, other studies suggest that temporal recency retrieval can recruit left PFC regions typically involved in attempts to recollect source or contextual information (Konishi et al., 2002; Suzuki et al., 2002). These latter studies used relatively short lists of study items (10–30 items/list) and manipulated the nature of recency decisions by comparing "high demand" Recency trials, in which test items had appeared close together in the original study list, with "low demand" Recency trials, in which test items had appeared farther apart at study (Konishi et al., 2002) or by comparing within-list recency decisions with between-list recency decisions (Suzuki et al., 2002). These latter studies suggest that the conditions that elicit activation in left PFC subregions are those that decrease subjects' ability to rely on marked differences in item familiarity as a basis for their recency judgments, thus demanding contextual recollection for accurate performance.

A complicating factor for understanding the relation between studies demonstrating increased left PFC activation during "demanding" recency conditions and those revealing right PFC activation during recency relative to item recognition judgments is the fact that a number of the studies in the latter group failed to match the nature of the test probes across conditions (Cabeza et al., 1997, 2000; Eyler Zorrilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996; Nyberg et al., 1996; Rajah & McIntosh, 2006; Suzuki et al., 2002). Specifically, the item memory test probes in these experiments contained novel items, whereas the temporal recency test probes consisted of studied items. Accordingly, the first objective of the current study was to investigate the pattern of PFC activation during temporal recency versus item recognition decisions, while ensuring that the test probes were matched across conditions. We further sought to directly compare the pattern of PFC activation during temporal recency decisions with that seen in prior studies of source recollection.

Beyond PFC, other data indicate that the medial temporal lobe (MTL) may differentially contribute to temporal recency and item recognition decisions. For example, rodent studies have suggested a distinct role of the hippocampus in encoding and retrieving the temporal order of a sequence of events (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002). In humans, some studies of patients with MTL lesions have demonstrated that such damage can disproportionately impair temporal-order memory in comparison to item recognition (Downes, Mayes, MacDonald, & Hunkin, 2002; Kopelman, Stanhope, & Kingsley, 1997; Mayes et al., 2001), whereas other studies have demonstrated either relatively spared temporal recency memory despite chance-level item memory (Sagar, Gabrieli, Sullivan, & Corkin, 1990) or impairments in both temporal-order memory and item recognition (Hopkins, Kesner, & Goldstein, 1995).

Recent neuroimaging evidence suggests that the MTL is recruited as recency retrieval demands increase (Konishi et al., 2002), as well as when recency decisions involve items that were studied in a relational as opposed to item-based manner (Konishi, Asari, Jimura, Chikazoe, & Miyashita, 2006). By contrast, other studies have revealed increased MTL activation during item recognition in comparison with temporal recency retrieval (Cabeza et al., 1997, 2000), though in these instances the comparisons of recency and item recognition trials were confounded by the presence of a novel item solely on item recognition trials. Because the MTL is known to differentially respond to the presence of novel stimuli (e.g., Dolan & Fletcher, 1997; Habib, McIntosh, Wheeler, & Tulving, 2003; Kirchhoff, Wagner, Maril, & Stern, 2000; O'Kane, Insler, & Wagner, 2005; Stark & Squire, 2001; Tulving, Markowitsch, Craik, Habib, & Houle, 1996), one interpretation for these latter effects is that the enhanced MTL responses during item recognition may have