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Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory

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ABSTRACT

The formation of episodic memories—memories for life events—is affected by attention during event processing. A leading neurobiological model of attention posits two separate yet interacting systems that depend on distinct regions in lateral posterior parietal cortex (PPC). From this dual-attention perspective, dorsal PPC is thought to support the goal-directed allocation of attention, whereas ventral PPC is thought to support reflexive orienting to information that automatically captures attention. To advance understanding of how parietal mechanisms may impact event encoding, we review functional MRI studies that document the relationship between lateral PPC activation during encoding and subsequent memory performance (e.g., later remembering or forgetting). This review reveals that (a) encoding-related activity is frequently observed in human lateral PPC, (b) increased activation in dorsal PPC is associated with later memory success, and (c) increased activation in ventral PPC predominantly correlates with later memory failure. From a dual-attention perspective, these findings suggest that allocating goal-directed attention during event processing increases the probability that the event will be remembered later, whereas the capture of reflexive attention during event processing may have negative consequences for event encoding. The prevalence of encoding-related activation in parietal cortex suggests that neurobiological models of episodic memory should consider how parietal-mediated attentional mechanisms regulate encoding.

1. Introduction

Episodic memory—conscious memory for life events—enables organisms to bridge the temporal gap between past and present (Tulving, 1985), allowing the past to inform present thought, decisions, and actions. During the last few decades, efforts to characterize the neural architecture of episodic memory have traditionally focused on mechanisms of the medial temporal lobe (MTL)—the hippocampus and adjacent medial temporal cortex—as well as those of the prefrontal cortex (PFC). While this focus is grounded in a rich literature documenting the negative consequences of MTL and PFC lesions on episodic memory (Scoville & Milner, 1957; reviewed in Eichenbaum, 2004; Ranganath & Knight, 2003; Shimamura, 1995; Squire, 1992), recent neuroimaging studies suggest that a complete story of the functional neurobiology of episodic memory may require appreciation of possible contributions from parietal cortex. This rapidly emerging neuroimaging literature indicates that dorsal and ventral regions of lateral posterior parietal cortex (PPC; Fig. 1) are consistently active during episodic *retrieval*. Now established functional dissociations between dorsal and ventral PPC during episodic remembering are beginning to shed new light on the neural and cognitive mechanisms underlying episodic retrieval (reviewed in Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005; for detailed anatomical boundaries, landmarks, and connectivity of PPC, see Olson and Berryhill, this issue).

At the same time, a growing body of evidence suggests that dorsal and ventral regions in lateral PPC are components of two dissociable, yet interacting, fronto-parietal attentional systems (e.g., Behrmann, Geng, & Shomstein, 2004; Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). From this dual-attention perspective, dorsal PPC regions—superior parietal lobule (SPL) and intraparietal sulcus (IPS)—mediate goal-directed or 'top-down' attention, whereas ventral PPC regions—inferior parietal lobule (IPL; comprised of supramarginal and angular gyri) and temporoparietal junction (TPJ)[1]—mediate stimulus-driven, reflexive, or 'bottom-up' attention. Anatomically, this dorsal/ventral PPC dissociation in the domain of attention qualitatively parallels the dorsal/ventral dissociation in PPC responses during episodic retrieval, motivating recent proposals articulating the role of goal-directed and reflexive 'attention to memory' during epi-

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[1] For the sake of consistency, here we hold to the definition of TPJ as defined by Corbetta, Patel, and Shulman (2008) as encompassing the area identified in Fig. 1 as the ventral portion of SMG.

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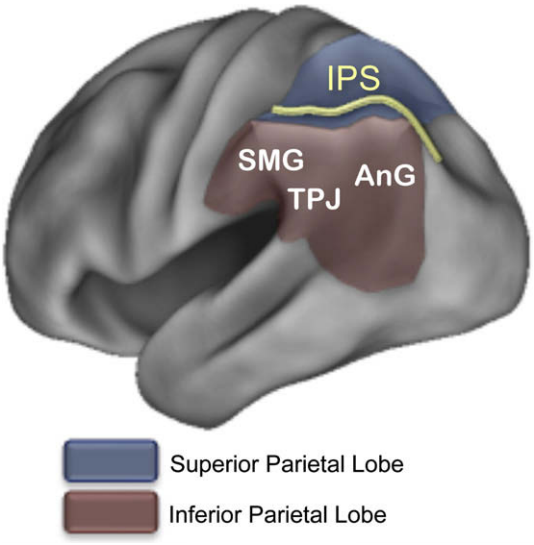

Fig. 1. Posterior parietal anatomy. Lateral posterior parietal cortex (PPC) is segregated into dorsal and ventral regions by the intraparietal sulcus (IPS). Dorsal regions include superior parietal lobe (SPL) and IPS, and ventral regions include aspects of inferior parietal lobe (IPL), namely supramarginal gyrus (SMG), temporoparietal junction (TPJ), and angular gyrus (AnG). Borders are drawn from projected borders of PALS-B12 fiducial atlas (Caret; Van Essen, 2005).

sodic retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008). While it remains possible that the correspondence between attention and episodic retrieval effects in PPC is more apparent than real (Hutchinson, Uncapher, & Wagner, submitted for publication), we view this cross-domain integrative theorizing as an important development for understanding the neural bases of episodic memory.

The ability to remember a past event is not only influenced by processes at retrieval, but also is predicated on processes engaged at the time of event encoding. While extensive behavioral evidence indicates that attention is a critical factor affecting episodic memory formation (Anderson & Craik, 1974; Baddeley, Lewis, Eldridge, & Thomson, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Kellogg, Bourne, & Cocklin, 1982; Moscovitch, 1992; Murdock, 1965; Park, Smith, Dudley, & Lafronza, 1989; for reviews see Chun & Turk-Browne, 2007; Craik, 2001), the neuroimaging literature examining the neural correlates of encoding has predominantly focused on the PFC and MTL. Given the dual-attention perspective on lateral PPC function and its possible implications for understanding episodic retrieval, here we take a parallel approach to explore the possibility that lateral PPC mechanisms may be more central to episodic *encoding* than previously assumed. In particular, we report a meta-analysis of lateral PPC findings from event-related functional magnetic resonance imaging (fMRI) studies investigating episodic encoding, focusing on studies that used the *subsequent memory paradigm* (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998; for review see Paller & Wagner, 2002) to relate encoding-stage neural activity with the subsequent mnemonic fate of an event (e.g., later remembered or forgotten). We first report the findings from this meta-analysis, and then propose a theoretical framework that describes possible contributions of lateral PPC mechanisms to episodic encoding. Throughout, we aim to connect this largely overlooked neuroimaging literature on lateral PPC activation during episodic encoding with that on lateral PPC mechanisms of goal-directed and reflexive attention.

2. Functional neuroimaging studies of encoding

Since the introduction of functional neuroimaging methods, study of the neural mechanisms of episodic encoding has advanced by means of various experimental paradigms. Early designs relied on comparing positron emission tomography (PET) or fMRI signals integrated across extended periods or 'blocks' of specific mental tasks. These blocked designs often varied the encoding tasks while holding constant the nature of the stimuli, or vice versa (for reviews see Buckner & Wheeler, 2001; Cabeza & Nyberg, 2000; Wagner, Koutstaal, & Schacter, 1999). For instance, candidate neural correlates of encoding were identified by contrasting the activity elicited by stimulus processing tasks yielding superior later memory with those yielding poorer later memory (i.e., 'levels of processing' manipulations; Craik & Lockhart, 1972; Craik & Tulving, 1975). Incidental encoding tasks that lead to superior memory generally include those where attention to stimulus meaning is required (e.g., semantic classification or self-reference judgments), whereas memory is typically poorer when more superficial aspects of stimuli are attended (e.g., judgments of phonology or, even more superficial attributes such as color, shape, or size). While studies employing levels-of-processing designs have predominantly emphasized that ventrolateral PFC activation is greater during meaningful vs. superficial orienting tasks (e.g. Demb et al., 1995; Gabrieli, Poldrack, & Desmond, 1998; Kapur et al., 1994), some studies have revealed the reverse pattern in PPC. For example, Wagner et al. (1998) observed greater activation in bilateral ventral and dorsal PPC during superficial vs. meaningful word processing (unpublished observations).

Another blocked-design approach is to directly vary the availability of stimulus-directed attention during encoding. It is well established that memory suffers when an encoding task is performed concurrently with a distracting task (e.g., Anderson & Craik, 1974; Baddeley, Scott, Drynan, & Smith, 1969; Baddeley et al., 1984; Murdock, 1965; for reviews see Craik, 2001; Yonelinas, 2002). This impairment may reflect the negative consequence of having fewer attentional resources to direct toward the to-be-encoded information. Given the importance of lateral PPC in theories of attention, it is surprising that, of the few blocked-design studies investigating the impact of divided-attention on neural correlates of encoding (e.g., Anderson et al., 2000; Fletcher, Shallice, & Dolan, 1998; Fletcher et al., 1995; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Shallice et al., 1994), only one reported an effect in lateral PPC. Specifically, Iidaka and colleagues (2000) observed increased activation in ventral PPC [~Brodmann's area (BA) 40] when volunteers intentionally encoded word pairs while performing a demanding vs. an easy secondary task.

The preceding between-condition comparisons in blocked-design studies provide a relatively indirect measure of encoding-related processing. A more direct blocked-design approach is to relate encoding activity during a block of study items to later memory performance, averaged across all of the items in the block. This approach has been implemented using both across- and within-subject analyses (Alkire, Haier, Fallon, & Cahill, 1998; Cahill et al., 1996; Fernandez et al., 1998, 1999). Notably, Alkire and colleagues (1998) reported that across-subject variability in ventral PPC activation (supramarginal and angular gyri, ~BAs 40 and 39, respectively) during encoding blocks positively correlated with the number of items later recalled from the blocks. This finding, when taken together with the levels-of-processing and divided-attention blocked-design literatures, provides limited but suggestive evidence for a role of lateral PPC in event encoding.

3. Subsequent memory methodology

Central to understanding episodic memory is delineation of the neurobiological processes that influence whether an individual event will be memorable or forgotten. Because blocked functional imaging designs provide measures of *average* activity over blocks