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Increased functional connectivity between dorsal posterior parietal and ventral occipitotemporal cortex during uncertain memory decisions

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ABSTRACT

Retrieval of episodic memories is a multi-component act that relies on numerous operations ranging from processing the retrieval cue, evaluating retrieved information, and selecting the appropriate response given the demands of the task. Motivated by a rich functional neuroimaging literature, recent theorizing about various computations at retrieval has focused on the role of posterior parietal cortex (PPC). In a potentially promising line of research, recent neuroimaging findings suggest that different subregions of dorsal PPC respond distinctly to different aspects of retrieval decisions, suggesting that better understanding of their contributions might shed light on the component processes of retrieval. In an attempt to understand the basic operations performed by dorsal PPC, we used functional MRI and functional connectivity analyses to examine how activation in, and connectivity between, dorsal PPC and ventral temporal regions representing retrieval cues varies as a function of retrieval decision uncertainty. Specifically, participants made a five-point recognition confidence judgment for a series of old and new visually presented words. Consistent with prior studies, memory-related activity patterns dissociated across left dorsal PPC subregions, with activity in the lateral IPS tracking the degree to which participants perceived an item to be old, whereas activity in the SPL increased as a function of decision uncertainty. Importantly, whole-brain functional connectivity analyses further revealed that SPL activity was more strongly correlated with that in the visual word-form area during uncertain relative to certain decisions. These data suggest that the involvement of SPL during episodic retrieval reflects, at least in part, the processing of the retrieval cue, perhaps in service of attempts to increase the mnemonic evidence elicited by the cue.

1. Introduction

Conscious memory for individual events from the past—episodic memory—is a powerful source for informing present decisions, large and small. The ability to incorporate information from past life episodes into an ongoing decision is critical for an organism to be able to avoid past mistakes and guide actions toward the optimal outcome. Despite the fundamental utility of retrieving episodic information from the past, much is still unsettled about the component cognitive and neurobiological operations that give rise to remembering.

One aspect of the cognitive neuroscience of remembering that has given rise to recent debate is how to interpret functional neuroimaging results that suggest that left posterior parietal cortex (PPC) is robustly engaged during episodic memory retrieval (Wagner, Shannon, Kahn, & Buckner, 2005). Specifically, numerous functional magnetic resonance imaging (fMRI) studies indicate that activity in multiple subregions of left lateral PPC is greater during the correct recognition of previously encountered items as old (i.e., hits) versus correct classification of novel items as new (i.e., correct rejections; for review, see Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Olson & Berryhill, 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). At a coarse anatomical level, it has been argued that activity in more dorsal PPC regions––the superior parietal lobe (SPL) and intra-parietal sulcus (IPS)––tracks the degree to which a memory probe is perceived as old (perhaps tracking perceived item familiarity, e.g. Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Sharot, Delgado, & Phelps, 2004; Wheeler & Buckner, 2004), whereas activity in ventral PPC––specifically, angular gyrus (AnG)––tracks the degree to which additional contextual details from the study episode are remembered (perhaps tracking recollection, e.g Cansino, Maquet, Dolan, &

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Rugg, 2002; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Kahn, Davachi, & Wagner, 2004; Kensinger & Schacter, 2006; Montaldi, Spencer, Roberts, & Mayes, 2006; Sharot et al., 2004; Wheeler & Buckner, 2004; Woodruff, Johnson, Uncapher, & Rugg, 2005).

While much initial interest focused on characterizing functional distinctions between dorsal and ventral PPC responses during episodic retrieval, recent findings suggest that within these coarse anatomical subdivisions, further functional distinctions are present. Of particular interest for the current study is the observation that retrieval activity in SPL is functionally dissociable from that in lateral IPS (Hutchinson, Uncapher, & Wagner, 2009; Hutchinson et al., 2014; Nelson et al., 2010; Sestieri, Shulman, & Corbetta, 2010). In particular, activity in SPL (and medial IPS) appears to vary with retrieval decision uncertainty, with elevated activity during slower or less confident memory decisions (Cabeza et al., 2008; Hutchinson et al., 2014; Sestieri et al., 2010), whereas activity in regions along the fundus and lateral bank of the IPS appears to increase in relation to the perceived oldness of the memory probe (e.g., Daselaar, Fleck, & Cabeza, 2006; Hutchinson et al., 2014).

Concurrent with the emergence of neuroimaging evidence for the multiple roles of dorsal PPC at retrieval has been a growing debate over how to best interpret these findings. This debate is complicated by the fact that on one hand dorsal PPC displays varied and meaningful sensitivity to key internal variables such as subjective memory strength and decision confidence during retrieval, but on the other hand it is also robustly engaged across a wide range of tasks designed to explore perception- and motor-related processes (e.g. Culham & Valyear, 2006; Silver & Kastner, 2009). Thus, many interpretations of the region's mechanistic role at retrieval have focused on its position at the intersection of internal and external processing. For example, some have posited that the region might serve to 'accumulate' mnemonic evidence (internal) in order to guide a particular decision (Wagner et al., 2005). Another interpretation posits that dorsal PPC performs similar operations of goal-directed ('top-down') attention across both internal (e.g., the retrieved contents of memory) and external (e.g., the perceptual cue used to probe memory) information (e.g. Cabeza, 2008; Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008).

Across both of these interpretations, there is a relatively unexplored common question concerning the nature of the representations with which dorsal PPC might interact during retrieval. That is, do the operations performed by dorsal PPC concern interactions with the external environment through, e.g., the perception of the retrieval probe or do they concern the processing of internal mnemonic signals more tightly linked to episodic retrieval? Moreover, are these operations differentially performed by different subregions of dorsal PPC?

The current experiment sought to further delineate the multifaceted contributions of dorsal PPC to episodic retrieval by assessing (a) the response profiles of dorsal PPC subregions in the face of decision uncertainty, and (b) which other regions of the brain respond in a similar fashion and functionally interact with dorsal PPC subregions. In particular, decision certainty during a recognition memory task was measured by having subjects make five-point confidence judgments about the old/new status of test cues. Critically, a series of fMRI analyses were performed to (1) further test whether SPL and lateral IPS demonstrate functionally dissociable activity profiles during recognition memory decisions, and (2) explore the degree to which dorsal PPC contributions to episodic memory might reflect internal or external processing. In particular, insofar as engagement of SPL reflects, at least in part, increased processing of the retrieval cue under uncertain retrieval decisions, we predicted that SPL would demonstrate increased functional coupling with regions in visual cortex that code for the visual aspects of the retrieval cue (also see Dobbins & Wagner, 2005).

2. Materials and methods

2.1. Participants

Thirty-five healthy adults participated in the study. Participants were right-handed, native English speakers, with no history of neurological disease or contraindications for MR imaging. Data from two participants were excluded due to imaging artifacts; data were also excluded from two participants due to excessive movement, and from five additional participants due to poor recognition memory (average $d' < 0.4$ across old/new and confidence judgment tasks) or insufficient number of trials in conditions of interest (5 or fewer trials). Accordingly, a total of 26 participants were included in the final data set (8 female, ages 19–28 yrs). Participants were paid $20/hr for the experiment, which lasted approximately 3.5 hrs. All participants gave informed, written consent in accordance with procedures approved by the institutional review board at Stanford University.

2.2. Materials

Stimuli consisted of 620 visually presented adjectives, taken from a corpus used in several previous fMRI studies (Davachi, Mitchell, & Wagner, 2003; Hutchinson et al., 2014; Kahn et al., 2004). The adjectives ranged in length from 3 to 10 letters (mean = 6.93). Twenty adjectives were used during a practice session. Of the 600 remaining items, 300 were presented during an encoding phase and served as old items during the retrieval phases, and 300 served as new items (foils) during retrieval. Old and new items were split evenly between two retrieval tasks (old/new and confidence judgment). Trial order was pseudo-randomized so as to not contain more than three consecutive trials of a given condition. The order of conditions was determined using an optimal sequencing algorithm that maximized the efficiency of the event-related design (OptSeq; Dale, 1999). The algorithm also determined the duration and frequency of null (fixation) events, which accounted for approximately 1/3 of trials. Across participants, stimuli were counterbalanced to be both studied and novel items at retrieval.

Stimulus presentation and collection of behavioral responses were implemented in Matlab, using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) running on an Apple MacBookPro laptop. During the non-scanned encoding phase, stimuli were centrally presented on the laptop monitor and responses (button presses) were made on the laptop keyboard. During the scanned memory retrieval phases, stimuli were projected onto a screen and viewed through a mirror on the head coil, and responses (button presses) were made using an MR-compatible response box. All responses in the experiment were made with the right hand.

2.3. Procedure

The experiment consisted of two phases: an incidental study phase administered outside of the scanner, and a test phase conducted during fMRI. The test phase consisted of two different tasks: a recognition confidence task followed by an old/new recognition task. The latter task (old/new recognition) was administered for a purpose irrelevant to the current study and will not be discussed further. Both study and test phases were preceded by a brief practice round containing a set of trials with identical structures to the actual task. The recognition confidence task was additionally preceded by a response training session, wherein participants prac-

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