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Reviews and perspectives

Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis

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Abstract

Although parietal cortex is frequently activated during episodic memory retrieval, damage to this region does not markedly impair episodic memory. To account for these and other findings, a new *dual attentional processes* (DAP) *hypothesis* is proposed. According to this hypothesis, dorsal parietal cortex (DPC) contributes top-down attentional processes guided by retrieval goals, whereas ventral parietal cortex (VPC) contributes bottom-up attentional processes captured by the retrieval output. Consistent with this hypothesis, DPC activity increases with retrieval effort whereas VPC activity increases with confidence in old and new responses. The DAP hypothesis can also account for the overlap of parietal activations across different cognitive domains and for opposing effects of parietal activity on encoding vs. retrieval. Finally, the DAP hypothesis explains why VPC lesions yield a *memory neglect syndrome*: a deficit in spontaneously reporting relevant memory details but not in accessing the same details when guided by specific questions.

Keywords: Memory; Episodic memory; Retrieval; Parietal; Attention; Top-down; Bottom-up; Confidence; Encoding; Working memory; Neglect; Recollection; Familiarity; Temporo-parietal junction; TPJ

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The role of lateral parietal regions in episodic memory retrieval is a very interesting cognitive neuroscience dilemma. On one hand, activations in these regions are among the most frequent in positron emission tomography (PET) and functional MRI (fMRI) studies of episodic retrieval (for a review, see Cabeza & Nyberg, 2000), whereas on the other hand, lesions in lateral parietal regions do not typically yield severe episodic memory deficits, such as the ones associated with medial temporal lobe (MTL) damage. This inconsistency may be only apparent, as there is now evidence that certain parietal lesions do in fact impair some forms of episodic memory (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). However, why episodic deficits following parietal damage are rare and why only certain forms of episodic memory are affected remain open questions. Moreover, functional neuroimaging evidence suggests that ventral and dorsal regions play different roles in episodic memory retrieval (Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). To address these issues, the current paper proposes a *dual attentional processes* (DAP) *hypothesis* that links the role of dorsal parietal cortex (DPC) and ventral parietal cortex (VPC) in episodic retrieval to their presumed roles in attention (Corbetta & Shulman, 2002). DPC is defined here as lateral parietal regions in or above the intraparietal sulcus (Brodmann Area 7), whereas VPC is defined as the supramarginal and angular gyri (Areas 40 and 39). Although medial parietal regions are also associated with episodic retrieval, they may involve different processes than lateral parietal regions, and are not considered in the present article. The paper consists of five main sections. The first section describes the DAP hypothesis; the second and third sections review functional neuroimaging and lesion evidence supporting this hypothesis, the fourth section considers open questions regarding the hypothesis, and the final section provides some conclusions.

1. Role of ventral and dorsal parietal regions in episodic retrieval

1.1. Three hypotheses on the role of parietal cortex and episodic retrieval

The review by Wagner et al. (2005) considered three hypotheses on the role of parietal regions in episodic retrieval. First, the *output buffer hypothesis* postulates that parietal regions hold retrieved information in a form accessible to decision-making processes, similarly to one of Baddeley's working memory buffers. Second, the *mnemonic accumulator hypothesis* posits that parietal regions temporally integrate a memory-strength signal. Wagner et al. (2005) linked this idea to signal-detection models of recognition memory that postulate that old–new memory decisions are determined by a continuous memory magnitude. Finally, the *attention to internal representation hypothesis* states that parietal regions shift attention to, or maintains attention on, internally generated mnemonic representations.

As noted by Wagner et al. (2005), each of these hypotheses can account for some but not all available functional neuroimaging evidence. The output buffer hypothesis fits well with evidence that certain parietal regions are associated with *recollection* (vivid remembering of an event including specific contextual details) rather than with *familiarity* (vague feeling of oldness in the absence of specific details) (e.g., Daselaar, Fleck, & Cabeza, 2006; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005). The idea is that these regions hold the *qualitative content* of retrieved information (e.g., mental images), which by definition are greater for recollection than for familiarity. However, the output buffer hypothesis cannot easily explain why activity in some parietal regions increases as a function of *perceived oldness*, which refers to the tendency to respond "old" regardless of the true nature of the stimuli (e.g., Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003). This finding fits better with the mnemonic accumulator hypothesis, which assumes that parietal regions do not hold actual memories but rather a signal summarizing information coming from other brain regions, which is eventually used to make memory decisions. Thus, these regions show high activity not only for "old" responses to old items (hits) but also for "old" responses to new items (false alarms). Nevertheless, the mnemonic accumulator hypothesis cannot readily accommodate evidence that certain parietal regions show greater activity when participants attempt to recollect source information than when they try to retrieve item information, regardless of responses and accuracy (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins & Wagner, 2005). This *recollective-orienting* pattern suggests that these regions track the intention to remember, that is, voluntary attention to memory contents, and hence, it fits well with the attention to internal representations hypothesis. Yet, voluntary attention cannot explain the aforementioned finding that some parietal regions show greater activity for recollection than for familiarity.

Given that all three hypotheses are partly correct, one possible solution is to expand one of them so it can accommodate a larger set of findings. One of the hypotheses that can be expanded is the attention to internal representation hypothesis. Although this hypothesis primarily focuses on goal-driven voluntary attention processes, not all forms of attention are voluntary. In fact, a fundamental distinction in the attention literature contrasts *top-down* (*or intentional*) *attention*, which is guided by goals and expectations, and *bottom-up* (*or reflexive*) *attention*, which is guided by the saliency of incoming information (for a review, see Yantis, 2000). Thus, it is reasonable to expand the attention account of parietal contributions to episodic retrieval so that it includes not only top-down attention but also bottom-up attention. This new hypothesis depends on the assumption that top-down and bottom-up attention are mediated by *different* parietal regions, which, as reviewed below, is an idea supported by functional neuroimaging and lesion evidence.

1.2. Dual attentional processes in parietal cortex

According to Corbetta and Shulman (2002), top-down attention is supported by a dorsal fronto-parietal system, whereas bottom-up attention is mediated by a ventral fronto-parietal sys-