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Research report

Parietal control network activation during memory tasks may be associated with the co-occurrence of externally and internally directed cognition: A cross-function meta-analysis

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ABSTRACT

Functional neuroimaging studies on episodic memory retrieval consistently indicated the activation of the precuneus (PCU), mid-cingulate cortex (MCC), and lateral intraparietal sulcus (latIPS) regions. Although studies typically interpreted these activations in terms of memory retrieval processes, resting-state functional connectivity data indicate that these regions are part of the frontoparietal control network, suggesting a more general, cross-functional role. In this regard, this study proposes a novel hypothesis which suggests that the parietal control network plays a strong role in accommodating the co-occurrence of externally directed cognition (EDC) and internally directed cognition (IDC), which are typically antagonistic to each other. To evaluate how well this dual cognitive processes hypothesis can account for parietal activation patterns during memory tasks, this study provides a cross-function meta-analysis involving 3 different memory paradigms, namely, retrieval success (hit > correct rejection), repetition enhancement (repeated > novel), and subsequent forgetting (forgotten > remembered). Common to these paradigms is that the target condition may involve both EDC (stimulus processing and motor responding) and IDC (intentional remembering, involuntary awareness of previous encounter, or task-unrelated thoughts) strongly, whereas the reference condition may involve EDC to a greater extent, but IDC to a lesser extent. Thus, the dual cognitive processes hypothesis predicts that each of these paradigms will activate similar, overlapping PCU, MCC, and latIPS regions. The results were fully consistent with the prediction, supporting the dual cognitive processes hypothesis. Evidence from relevant prior studies suggests that the dual cognitive processes hypothesis may also apply to non-memory domain tasks.

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1. Introduction

1.1. Parietal contribution to retrieval success

A fundamental component of episodic memory retrieval is the ability to distinguish previously encountered events from novel ones, i.e., to identify events as old or new. To investigate the neural correlates of this ability, functional neuroimaging studies com-

pared the neural activity that occurred when a studied item was correctly recognized (a hit) to that when a non-studied item was correctly rejected (a correct rejection). The associated results were typically termed "retrieval success" or "old/new" effects and associated with widely dispersed frontoparietal regions (see Kim (2013) for a meta-analysis). Of particular interest here is their strong association with 3 parietal regions, namely, the precuneus (PCU), mid-cingulate cortex (MCC; anterior extent of Brodmann area [BA] 23, 31), and lateral intraparietal sulcus (latIPS). Numerous studies (e.g., Donaldson et al., 2010; Elman et al., 2013; Henson et al., 2000; Konishi et al., 2000; Shannon and Buckner, 2004; Thakral et al., 2015) demonstrated that these regions exhibited robust retrieval success effects across diverse experimental manipulations, including item and source memory, verbal and pictorial memory, and visual and auditory memory tasks. Although the involvement of the 3 parietal regions in episodic memory

retrieval processes is not in doubt, the issue of how they contribute to the processes remains largely unresolved. At least five different, potentially relevant hypotheses have been proposed.

First, a recent review (Gilmore et al., 2015) made valuable contributions to the field by calling attention to the fact that the 3 parietal regions were consistently involved in the retrieval success effect and other memory-related ones. This contribution is particularly noteworthy because previous discussions of parietal memory effects (e.g., Cabeza et al., 2008; Ciaramelli et al., 2008; Jaeger et al., 2013; O'Connor et al., 2010 Shimamura, 2011; Vilberg and Rugg, 2008) focused predominantly on the lateral parietal cortex, especially its ventral extent, despite the fact that other lateral/medial parietal regions also showed reliable memory-related effects. Based on the broad involvement of the 3 parietal regions in memory retrieval and their functional connectivity, the authors proposed that these 3 regions constituted a parietal memory network (PMN). Regarding its specific mnemonic function, they proposed that its activation signaled familiarity, whereas its deactivation signaled novelty, based in part on evidence that spatially similar regions tended to track familiarity or memory strength (Daselaar et al., 2006; Hutchinson et al., 2015; Yonelinas et al., 2005). However, a critical disadvantage of the familiarity/novelty-based hypothesis is that it tends to be descriptive of old/new effects rather than explaining them, limiting its predictive value.

A second hypothesis assumes that the participants in a recognition memory test expect to see new items (non-targets) rather than old items (targets) (Herron et al., 2004; Jaeger et al., 2013; Vilberg and Rugg, 2009). In order to make a correct 'old' decision, they need to countermand this presumption that the items are new, which likely exerts a high demand on the control functions, thereby eliciting greater activity for old than new items (O'Connor et al., 2010). A key prediction of this hypothesis is that increasing the ratio of old to new test items (e.g., from 25:75 to 75:25) would decrease the retrieval success effect. Previous studies (Herron et al., 2004; Vilberg and Rugg, 2009) showed that this prediction held strongly for some lateral frontal and other selective regions, but did not hold for the PCU, MCC, and latIPS regions, indicating that the 'expectancy violation' does not provide an adequate explanation for the involvement of these 3 regions in the retrieval success effect.

A seminal review paper by Wagner et al. (2005) considered three different hypotheses that potentially linked the parietal cortex to retrieval functions: (a) they support attention directed at internal, mnemonic representations, (b) they act as a memory buffer that actively represents retrieved information, and (c) they participate in the accumulation of mnemonic evidence in association with memory decision processes. Recognition memory can be based either on the vivid recall of an item with detailed contextual information, or *recollection*, or only on a vague feeling of oldness in the absence of any contextual details, or *familiarity* (for a review, see Yonelinas, 2002). A key prediction of the internal attention hypothesis is that relevant regions would show greater activity for recollection than for familiarity, because vivid memories would capture attentional resources more strongly than vague ones (Cabeza et al., 2008). The memory buffer hypothesis makes a similar prediction, because vivid memories would involve a greater amount of retrieved memories than vague ones (Vilberg and Rugg, 2008). Previous studies (Cabeza et al., 2008; Ciaramelli et al., 2008; Kim, 2010; Vilberg and Rugg, 2008) showed that although this prediction fared well in the case of the parietal subregions of the default mode network, that is, the inferior parietal cortex and posterior cingulate cortex/retrosplenial cortex regions, it did not hold in the case of the PCU, MCC, or latIPS regions.

As regards the mnemonic accumulation hypothesis, the PCU, MCC, and latIPS regions typically respond more strongly to old than new items, even when old/new decisions are not required (Donaldson et al., 2001; Kouider et al., 2009; Wang et al., 2016). This hypothesis cannot easily accommodate this finding, because mnemonic accumulation is hypothesized in association with memory decision processes (Sestieri et al., 2017; Wagner et al., 2005). Thus, none of the five hypotheses provide a fully satisfactory account of how the PCU, MCC, and latIPS regions contribute to memory retrieval processes.

1.2. The parietal control network

Numerous resting-state functional connectivity (RSFC) studies (e.g., Doucet et al., 2011; Power et al., 2011; Rosen et al., 2016; Smith et al., 2013; Vincent et al., 2008; Yeo et al., 2011) showed that the PCU, MCC, and latIPS regions are functionally connected (see Gilmore et al. (2015) for a review), making it easier to recognize the significance of congruent spatial patterns in task-based studies (Power et al., 2014). In coarse network estimates, the 3 parietal regions emerge as part of the frontoparietal control network (FPCN; see Fig. 1A and B for examples), but in more fine-grained estimates, they are separated from the frontal components, suggesting that they form a subnetwork within the frontoparietal control system. For example, an independent component analysis (ICA) of resting-state data with a relatively high dimensionality ($n = 23$) identified a network that only consisted of the PCU, MCC, and latIPS regions (Doucet et al., 2011; see Fig. 1C). In Yeo et al.'s (2011) clustering analysis of resting-state data, a 17-network, but not 7-network, parcellation isolated a network that only included the PCU and MCC regions. A recent RSFC analysis focusing on the parietal components of the FPCN indicated that the PCU was the local hub and that the latIPS linked the subnetwork with the rest of the FPCN (Rosen et al., 2016). In this regard, the separation of the latIPS from the PCU and MCC in Yeo et al.'s 17 network parcellation may reflect a role of this region in interfacing between subnetworks within the FPCN.

Because the PCU, MCC, and latIPS regions are relatively sparse, their activation has sometimes been ascribed to their adjoining regions, most typically the parietal subregions of the default mode network (e.g., Huijbers et al., 2013; Kim, 2013; Maillet and Rajah, 2014; Weissman et al., 2006). For example, the author's own previous interpretation of the involvement of the posteromedial regions in the retrieval success effect emphasized the default mode network (Kim, 2013). However, in hindsight, the local topography of the effect matched the FPCN more convincingly than the default mode network, because the effect extensively involved the MCC and PCU, but only marginally overlapped the posteromedial component of the default mode network. As may be seen in Fig. 1, the MCC/PCU and the posterior cingulate cortex/retrosplenial cortex are connectionally distinct, and show differential developmental trajectories across the lifespan (Yang et al., 2014).

The functional connectivity patterns of the PCU, MCC, and latIPS regions suggest that their activation may not be specific to mnemonic processing, but mediate more general control functions that potentially contribute to both memory and non-memory tasks. Indeed, there is strong evidence that they could be activated in association with a large range of cognitive tasks. Dosenbach et al. (2006) conjointly analyzed the brain activity from 10 different cognitive tasks (e.g., letter identification, reading, living/nonliving judgment, timing finger taps), none of which explicitly required episodic retrieval. Their analyses of activity contingent upon cues that signaled the beginning of a task block showed the involvement of the PCU, MCC, and latIPS and other FPCN regions across a majority of the tasks, suggesting that they played a crucial role in instantiating goal-directed task-sets. Igelström et al. (2016) investigated activity during five different cognitive tasks: theory-of-mind, episodic memory retrieval, social attribution of attention,