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A parietal memory network revealed by multiple MRI methods

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The manner by which the human brain learns and recognizes stimuli is a matter of ongoing investigation. Through examination of meta-analyses of task-based functional MRI and resting state functional connectivity MRI, we identified a novel network strongly related to learning and memory. Activity within this network at encoding predicts subsequent item memory, and at retrieval differs for recognized and unrecognized items. The direction of activity flips as a function of recent history: from deactivation for novel stimuli to activation for stimuli that are familiar due to recent exposure. We term this network the 'parietal memory network' (PMN) to reflect its broad involvement in human memory processing. We provide a preliminary framework for understanding the key functional properties of the network.

Parietal cortex contributes to memory processing in multiple ways

Since the earliest days of functional neuroimaging, researchers have sought to discover how the brain builds, and later accesses, memories. How one might predict whether a given experience would be remembered or forgotten [1,2], and how successful and unsuccessful retrieval differed in their neural signatures [3], were among the first questions asked by scientists when it became possible to isolate activity to single events or classes of events. Many of the answers, it turns out, are a rather unsatisfying 'it depends'. The neural correlates of successful encoding vary as a function of the type of initial study [4] or later retrieval task [5], while the correlates of successful retrieval differ as a function of how one's memory is tested, and typically appear in regions distinct from those implicated in encoding (e.g., [6–9]). In this review we identify a network of brain regions that demonstrates both encoding- and retrieval-related signals that appear to generalize across task conditions. We review evidence suggesting that the activity of this network reflects a continuum of how novel or how familiar a stimulus is perceived to be, and we discuss the importance of this network in advancing understanding of neural mechanisms related to learning and memory.

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Although early neuroimaging studies focused on the medial temporal and frontal lobes, parietal cortex has consistently been linked to human memory processing [10,11]. Numerous studies have associated parietal cortex with retrieval-success effects (see Glossary) [12–15], but regions of parietal cortex also show differential activity for: (i) subsequently forgotten, relative to subsequently remembered, items during memory encoding [16,17]; (ii) intentional retrieval tasks relative to intentional encoding tasks [18]; (iii) items that have been encoded multiple times relative to items that are encoded for the first time [19,20]; (iv) false alarms (new items judged as old) relative to misses (old items judged to be new) [21]; (v) more confidently, relative to less confidently, retrieved items [6]; and (vi) items for which rich, relative to sparse, contextual information is accessible at retrieval [7,22].

Hypotheses have been forwarded to explain these different patterns of data (see [10,23] for reviews), but no single hypothesis can account for all of the patterns

Glossary

Encoding-retrieval flip: a regional BOLD response pattern in which the direction of evoked activity, relative to resting baseline, flips between encoding and retrieval. Typically this pattern is observed in encoding-induced deactivations and retrieval-induced activations.

Functional network: a group of brain regions that coactivate during particular types of task or task conditions and that show highly correlated spontaneous activity in the absence of explicit task conditions (i.e., during the 'resting-state').

Repetition enhancement: repetition enhancement involves an increase in neural activity across multiple presentations of an item. Such effects have received fairly little attention in comparison to the reverse situation, repetition suppression, in which repeated presentations of stimuli elicit reductions in observed neural activity.

Resting-state functional connectivity MRI: an fMRI-based technique to assess the functional relatedness of different regions of cortex, in the absence of any explicit task conditions; that is, the participant lies still and passively stares at a fixation cross or closes their eyes. High correlations between regions are thought to reflect a history of coactivation across one's lifetime.

Retrieval-success effect: regional differences in average activity, during retrieval, for items that are successfully retrieved as compared to those that are not. Within the realm of recognition memory, retrieval-success effects take the form of greater activity for correctly recognized old items ('hits') as compared to correctly identified new items ('correct rejects') or less frequently, incorrectly classified old items ('misses').

Subsequent memory effect: regional differences in average activity, during encoding, for items that are later retrieved on a memory test relative to those that are forgotten. This pattern typically emerges as greater activity for items that are later recognized. Negative subsequent memory (nSM) effects show the reverse of this pattern, with less activity for items that are later recognized relative to those later missed; specifically, this latter pattern is often revealed in greater deactivation for items later recognized relative to those later missed. nSM effects are sometimes called 'subsequent forgetting' effects.

described above. In part, this is because these hypotheses focus primarily on retrieval [17]. In addition, they mainly focus on lateral parietal cortex, with less consideration of medial parietal cortex, which is also strongly linked to memory (e.g., [18,24,25]). Further, lateral parietal cortex is heterogeneous, composed of a mosaic of distinct functional areas, each with its own pattern of connectivity and each with its own functional response profile during memory tasks ([26–29], but see also [11,30]). The network we highlight in this report consists of both medial and lateral parietal regions that are involved in multiple stages of memory processing. Identification of this small collection of regions, and the claim that they form a functional network, emerged from two distinct analysis approaches, described below.

Three parietal regions consistently support memory functioning

Meta-analyses identify regions most consistently associated with a condition of interest, and allow trends across many studies to emerge over the peculiarities specific to any individual dataset. Meta-analyses of encoding- and retrieval-related effects have each implicated the precuneus (PCU), the mid-cingulate cortex (MCC), and the posterior inferior parietal lobule/dorsal angular gyrus (pIPL/dAG; Figure 1). The MCC region would be characterized by some as 'posterior cingulate cortex', but we use the term MCC to help differentiate it from the adjacent, well-known posterior cingulate regions reported in other contexts (e.g., [31,32]). The three regions are among those most consistently associated with retrieval success

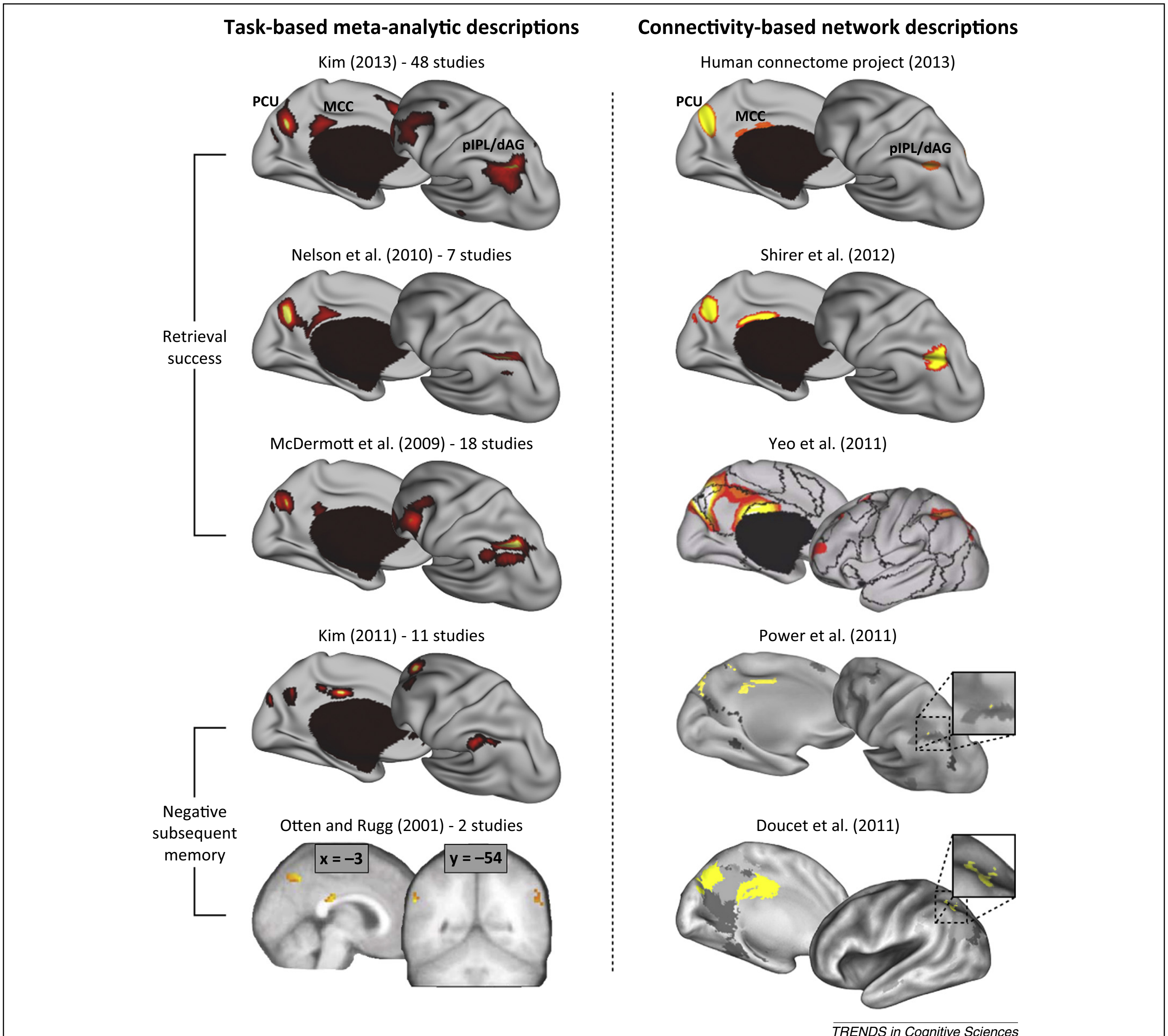

Figure 1. Task-based and functional connectivity descriptions of a parietal memory network. (Left column) Task-based meta-analyses highlight the consistent recruitment of the precuneus (PCU), mid-cingulate cortex (MCC), and posterior inferior parietal lobule/dorsal angular gyrus (pIPL/dAG) in memory encoding and retrieval tasks. (Right column) Five independent datasets based on functional connectivity analyses identify the same regions as being members of a distinct functional network. Data from [8,9,16,26,39,71] are taken from their respective publications, and projected onto brain surfaces using Connectome Workbench software [74]. Remaining maps are adapted from [33,36–38] with permission from Elsevier and the American Physiological Society.