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Some surprising findings on the involvement of the parietal lobe in human memory

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ABSTRACT

The posterior parietal lobe is known to play some role in a far-flung list of mental processes: linking vision to action (saccadic eye movements, reaching, grasping), attending to visual space, numerical calculation, and mental rotation. Here, we review findings from humans and monkeys that illuminate an untraditional function of this region: memory. Our review draws on neuroimaging findings that have repeatedly identified parietal lobe activations associated with short-term or working memory and episodic memory. We also discuss recent neuropsychological findings showing that individuals with parietal lobe damage exhibit both working memory and long-term memory deficits. These deficits are not ubiquitous; they are only evident under certain retrieval demands. Our review elaborates on these findings and evaluates various theories about the mechanistic role of the posterior parietal lobe in memory. The available data point towards the conclusion that the posterior parietal lobe plays an important role in memory retrieval irrespective of elapsed time. However, the available data do not support simple dichotomies such as recall versus recognition, working versus long-term memory. We conclude by formalizing several open questions that are intended to encourage future research in this rapidly developing area of memory research.

1. Introduction

If you were to peruse any textbook on memory or neuroscience, you would be hard-pressed to find the terms "memory" and "parietal lobe" together. How then, do we explain the large number of neuroimaging findings reporting parietal lobe activations to various mnemonic demands? The sheer volume of these findings raises the question of whether the parietal lobe plays a functional role in mnemonic processing that has been overlooked.

To address this question, we review evidence linking the parietal lobe to memory. We focus on visual short-term or working memory (WM) and episodic memory for the simple reason that there is now sufficient material in these literatures to provide some nascent consensus. We note that links between verbal WM and parietal lobe function has recently been reviewed elsewhere (Buchsbaum & D'Esposito, 2008).

Our first piece of evidence that the parietal lobe may have some role in memory comes from white matter tractography revealing close anatomical linkages between the parietal lobe and frontal and medial temporal lobe areas. Subsequent sections describe experimental evidence from visual WM, object WM and episodic memory studies. We explore various hypotheses describing the mechanism of parietal involvement in memory and conclude with a series of open questions meriting further research.

2. Anatomy and connectivity of the posterior parietal cortex

Because in vivo axon tracing techniques cannot be applied to humans, much of our knowledge of the connectivity of the parietal lobe is drawn from work in non-human primates. This presents us with a significant intellectual hurdle, since the extent of inter-species homology is unclear (Culham & Kanwisher, 2001; Glover, 2004), but see (Rushworth, Behrens, & Johansen-Berg, 2006). The human parietal lobe is nearly 20 times larger than that of the macaque. This ratio is markedly higher than the same comparison made between human and macaque temporal (9 times larger), or occipital (2 times larger) cortices (Van Essen et al., 2001). The size difference is partially explained by the expansion of the human inferior parietal lobe. Indeed, there appears to be no equivalent of the human supramarginal gyrus (BA 39) in monkeys (Karnath, Ferber, & Himmelbach, 2001). Despite this problem, there are some parietal regions that appear to share anatomical and functional similarities between macaques and humans (Culham & Valyear, 2006) and more recent non-invasive functional connectivity studies are beginning to provide information about human parietal connectivity (Rushworth et al., 2006).

Beginning anteriorly, the human parietal lobe is located immediately posterior to the central sulcus, where the somatosensory

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cortices (Brodmann areas (BA) 1, 2, and 3) occupy the postcentral sulcus. More posterior regions, referred to herein as the posterior parietal cortex (PPC) are traditionally divided into the superior parietal lobe (SPL; BA 5 and 7), the medial parietal lobe (mesial extent of BA 7), and the inferior parietal lobe (IPL; BA 39 and 40).[1] The SPL is posterior to somatosensory cortex and above the intraparietal sulcus (IPS), excluding medial parietal cortex. The medial parietal lobe consists primarily of the precuneus, which is buried in the interhemispheric fissure. Recently some authors have defined the medial parietal cortex very inclusively, including the limbic posterior cingulate and retrosplenial cortices in their definitions of this region (Vincent et al., 2006). Here, we hold to the more traditional definition of medial parietal cortex. The IPL is located below the horizontal portion of the IPS, anterior to the superior occipital lobe, and consists of the angular (BA 39) and the supramarginal gyri (BA 40).

2.1. Inferior parietal lobe and medial temporal lobe connectivity

In 1957, Scoville and Milner reported that bilateral damage to the human medial temporal lobe causes chronic anterograde amnesia (Scoville & Milner, 1957). We now know that within the medial temporal lobe (MTL), the hippocampus plays a central role in spatial and episodic memory formation. Monkey tractography studies have identified two large axons tracts connecting the IPL to the medial temporal lobe. First, portions of the inferior longitudinal fasciculus connect the angular gyrus with the parahippocampal gyrus (Seltzer & Pandya, 1984). Second, the cingulum bundle, which lies within the cingulate cortex, connects lateral and medial regions of the posterior IPL (PG and Opt[2] to the parahippocampal gyrus (Seltzer & Pandya, 1984). Connections also exist between entorhinal cortex and IPL area 7 in the monkey (Insausti & Amaral, 2008; Wellman & Rockland, 1997). Most interestingly, there are connections between area CA1 in the anterior portion of the hippocampus and area 7a, in the posterior IPL of the monkey (also known as PG or Opt) (Clower, West, Lynch, & Strick, 2001; Rockland & Van Hoesen, 1999) and 7b, found in the anterior IPL (also known as area PF) of the monkey (Rockland & Van Hoesen, 1999). Information flow is predominantly directly from CA1 to 7a, suggesting that memory functions of the hippocampus modulate processing in area 7a (Clower et al., 2001) (see Fig. 1A). Connections have also been identified between the presubiculum and area 7a (Cavada & Goldman-Rakic, 1989; Ding, Van Hoesen, & Rockland, 2000.)

Although these findings are predominantly based on investigations of monkey anatomy, there is some evidence that the human inferior parietal lobe has similar patterns of MTL connectivity. Rushworth and colleagues, using a diffusion weighted tractography method, reported a pattern of connectivity between a region of the parahippocampal gyrus just lateral to the hippocampus and the angular gyrus that resembled the inferior longitudinal fasciculus (see Fig. 1C). The angular gyrus in the IPL was the only lateral parietal region with a high probability of connection to the parahippocampus (Rushworth et al., 2006). In addition, resting state fluctuations in the BOLD signal show correlations between the hippocampus and medial–lateral PPC (Vincent et al., 2006; see also Greicius & Menon, 2004; Takahashi, Ohki, & Kim, 2008).

2.2. Superior and inferior parietal–frontal connectivity

Portions of the frontal lobe are known to play a critical supporting role in mnemonic functions. In the monkey, several large fiber tracts connect both inferior and superior parietal regions to the prefrontal cortex. The dominant white matter tract connecting these regions is the superior longitudinal fasciculus (SLF). The SLF can be divided into three subcomponents from the most superior to the most inferior: SLF I, SLF II, SLF III (Makris et al., 2005; Schmahmann et al., 2007) (see Fig. 1B). The SLF I connects medial and dorsal portions of the SPL (part of areas PE, PG, 31) to dorsal premotor and prefrontal regions (BA 6 and 9, supplementary motor area) (Schmahmann & Pandya, 2006; Schmahmann et al., 2007) and is most likely important for higher order motor behavior (Petrides & Pandya, 2006). The SLF II unites the posterior IPL (area PO in the IPS, PG, Opt) with the mid- and dorsolateral prefrontal cortices (BA 6, 8, 9, 46) (Schmahmann & Pandya, 2006; Schmahmann et al., 2007). The fronto-occipital fasciculus links a broad swath of medial (areas PO, PG medial) and posterior IPL regions (areas PG lateral, Opt, DP) with a band of regions in dorsolateral prefrontal cortex (areas 6D, 8Ad, 8B, 9, 46d) (Schmahmann & Pandya, 2006). SLF III connects the anterior inferior parietal lobe (region PF/PO of the IPS) and the anterior intraparietal area within the IPS, with ventral premotor, ventral prefrontal, and dorsolateral prefrontal cortex (areas 6,44, 9/46) (Schmahmann & Pandya, 2006; Schmahmann et al., 2007). The function of these tracts is unknown, although it has been suggested that they are important for visual attention and working memory (Cavada & Goldman-Rakic, 1989; Schmahmann et al., 2007). Last, a separate axon tract, the cingulum bundle (temporal aspects only) links posterior IPL (area PG, Opt) to the supplementary motor area and the dorsolateral prefrontal cortex (Mori, 2005). The cingulum bundle is considered the "dorsal limbic pathway" as it has branches that extend not only throughout the length of the cingulate, but also to the hippocampus and parahippocampus (Seltzer & Pandya, 1984). Thus, via the cingulum bundle, the posterior IPL is connected both to the dorsolateral prefrontal cortex and to the hippocampus.

3. Working memory for spatial attributes

Over 50 years ago MacDonald Critchley remarked "*Bilateral disease of the brain, and especially of the parieto-occipital regions, may be followed by the most conspicuous spatial disorders, especially entailing visual disorientation.*" (Critchley, 1953, p. 354). Of the many spatial processes linked to parietal lobe function, spatial WM is a more recent addition. This type of memory allows one to remember spatial information over short delay periods—where one looked a few moments ago, for instance. There are several sources of evidence linking the parietal lobe to spatial working memory: neurophysiological, neuropsychological, brain imaging, and transcranial magnetic stimulation (TMS).

"Memory cells" are cells that display persistent activity during the delay period of a WM task. The discharge of memory cells is higher during the delay period than during baseline periods between trials. Such cells were first found in the dorsolateral prefrontal cortex (PFC) of monkeys performing spatial WM tasks (Fuster & Alexander, 1970; Niki & Watanabe, 1976). Since their discovery, memory cells have also been found in other brain regions including the lateral intraparietal cortex in the PPC (Gnadt & Andersen, 1988; Mazzoni, Bracewell, Barash, & Andersen, 1996). PPC memory cells also exhibit delay activity during spatial WM tasks (Constantinidis & Steinmetz, 1996; Fuster, 1990; Gnadt & Andersen, 1988, reviewed inConstantinidis, 2006; Constantinidis & Procyk, 2004; Constantinidis & Wang, 2004) that is comparable

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[1] An alternative anatomical nomenclature divides the posterior parietal lobe into dorsal and ventral regions. The dorsal parietal lobe corresponds to the lateral and medial parts of BA 7, the ventral parietal lobe corresponds to the inferior parietal lobe.

[2] The anatomical terms PG, PF, Opt, 7a, and 7b are used primarily by monkey researchers following von Economo's terminology (von Economo & Koskinas, 1925).