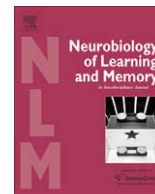




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Some surprising findings on the involvement of the parietal lobe in human memory

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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.

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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 (Buchsbbaum & 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 Opt² 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).

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).

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 in Constantinidis, 2006; Constantinidis & Procyk, 2004; Constantinidis & Wang, 2004) that is comparable

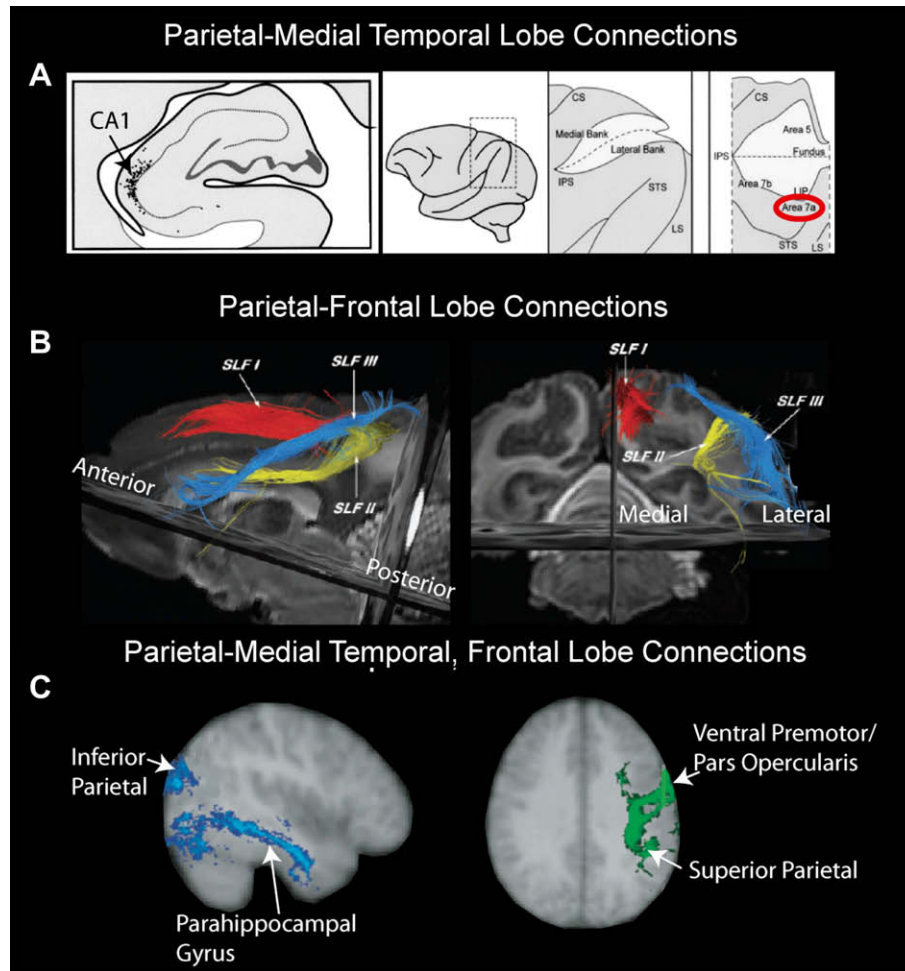


Fig. 1. Parietal–medial temporal lobe connections. (A) Hippocampal area CA1 (black dots in left-most panel) projects to area 7a (demarked with an oval in the right-most panel) in the lateral intraparietal area (LIP), as shown by retrograde viral tracing in the cebus monkey (Clower et al., 2001). The middle figures provide anatomical orientation for monkey area 7a. (B) Parietal–frontal lobe connections. The three branches of the macaque superior longitudinal fasciculus (SLF I–III) are shown from two perspectives: on the left, the lateral view and on the right the coronal view demonstrating the medial connections and the lateral connections (Schmahmann et al., 2007). (C) Human diffusion weighted tractography. The left panel shows the results of a human diffusion weighted tractography study in which broad connections between inferior parietal regions and the whole of the parahippocampal gyrus (left panel), and connections between superior parietal and frontal areas (right panel) were found (Rushworth et al., 2006). Figures taken with kind permission from the publishers.

to delay activity observed in PFC neurons (Fuster, 1984). Selective cooling of areas 5 and 7 disrupts spatial memory (Quintana & Fuster, 1993).

In accord with these findings, it has been known for several decades that damage to the right PPC in humans leads to impaired spatial WM. Spatial WM deficits subsequent to PPC damage are observed across a range of tasks and stimuli (see Table 1) such as old/new recognition of simultaneously or sequentially presented locations (Berryhill & Olson, 2008b; Husain et al., 2001; Malhotra et al., 2005; Pisella, Berberovic, & Mattingley, 2004), or recall, by pointing, to a series of locations (Baldo & Dronkers, 2006; De Renzi, Faglioni, & Previdi, 1977; De Renzi & Nichelli, 1975; Hanley, Young, & Pearson, 1991; Malhotra et al., 2005).

It is important to bear in mind that IPL lesions, near the temporo-parietal junction frequently result in hemispatial neglect (Vallar & Perani, 1986). Hemispatial neglect is a heterogeneous disorder (Shimozaki, Kingstone, Olk, Stowe, & Eckstein, 2006, reviewed in Buxbaum, 2006; Driver & Vuilleumier, 2001; Ellis, Della Sala, & Logie, 1996; Halligan, Fink, Marshall, & Vallar, 2003; Heilman, Jeong, & Finney, 2004; Heilman, Valenstein, & Watson, 2000; Hillis, 2006; Pisella & Mattingley, 2004) characterized by a failure to at-

tend, react to, or to perceive stimuli presented in the contralesional visual field. Spatial WM deficits are known to occur in patients with hemispatial neglect. For instance, several recent studies of neglect patients required subjects to remember sequentially presented locations arrayed in a vertical line. The results showed that neglect patients had impaired spatial WM performance (Malhotra, Mannan, Driver, & Husain, 2004; Malhotra et al., 2005; Parton et al., 2006). When the eye movements of neglect patients were assessed in visual search tasks, it was shown that they tend to revisit previously foveated items as if they were new items, indicative of a spatial WM impairment (Husain et al., 2001; Wojciulik, Husain, Clarke, & Driver, 2001). After neglect resolves (or even if it never existed), spatial WM deficits remain present (see Table 1), indicating that the spatial WM deficits are not attributable to inattentiveness to portions of space. Converging evidence for the importance of the right PPC in spatial WM is offered by several TMS studies showing that transient inactivation of these regions impairs spatial WM (Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000; Koch et al., 2005; Oliveri et al., 2001).

Neuroimaging studies have overwhelmingly corroborated these findings (D'Esposito et al., 1998; Hartley & Speer, 2000; Smith &

Table 1
Neuropsychological studies of spatial working memory as assessed by recall or recognition in patients with putative parietal lobe damage

Authors	Task	Lesion sites	Spared	Impaired
De Renzi and Nichelli (1975)	Recall: Corsi	L hemi, R hemi		✓
De Renzi et al. (1977)	Recall: Corsi	R hemi, R hemi with visual field defect		✓
Hanley et al. (1991)	Recall: Corsi	R hemi , (case study)		✓
Markowitsch et al. (1999)	Recall: Corsi	L angular gyrus, Case	✓	
Della Sala, Gray, Baddeley, Allamano, and Wilson (1999)	Recall: Pattern Span, Corsi	R hemi, L hemi, Bi hemi	✓	
Kessels et al. (2000)	Recall: Corsi	R hemi , L hemi, Bi hemi, subcortical		✓
Postma, Sterken, de Vries, and de Haan (2000)	Recall: Perceptual Localization (2AFC)	R hemi, L hemi		✓
Kessels, Jaap Kappelle, de Haan, and Postma (2002)	Recall: Object-Location Conjunction, Locations, Corsi, Maze learning	L hemi, R hemi , Bi hemi, Anterior (frontal, temporal), Posterior (occipital, parietal)	✓ *Corsi block	✓ *conjunction task
Pisella et al. (2004)	Old/new recognition	R PPC + neglect , non-PPC + neglect		✓
Malhotra et al. (2005)	Recall Old/new Recognition: Vertical Corsi	R PPC + neglect ; R PPC non-neglect		✓
van Asselen et al. (2006)	Recall: Corsi	R PFC, L PFC, R PPC, L PPC	✓	
Nys, van Zandvoort, van der Worp, Kappelle, and de Haan (2006)	Recall: Corsi	R hemi + neglect, L hemi + neglect, Bi hemi + neglect ,		✓
Baldo and Dronkers (2006)	Recall: Corsi	L inf PPC , L inf frontal		✓
Berryhill and Olson (2008b)	Old/new recognition: locations	R PPC		✓
Ferber and Danckert (2006)	Old/new recognition: Vertical locations	R PPC + neglect , R PPC		✓
Vuilleumier et al. (2007)	Old/new recognition	R PPC + neglect		✓
Husain et al. (2001)	Visual search revisiting	R PPC + neglect , R PPC		✓
Parton et al. (2006)	Visual search revisiting	R PPC + neglect , R PPC		✓
Mannan et al. (2005)	Visual search revisiting	R PPC (by lesion location) + neglect		✓

Note that in many studies precise cerebral localization was not provided. Highlighted text in the lesion site column indicates which patient population, if any, was impaired. Abbreviations: Bi, bilateral; Corsi, Corsi block-tapping task; hemi, hemisphere; inf, inferior; L, left; R, right; PPC, posterior parietal cortex; PFC, prefrontal cortex; 2AFC, two-alternative forced-choice.

Jonides, 1997; Smith & Jonides, 1998; Ungerleider, Courtney, & Haxby, 1998). More recent event-related fMRI findings suggest that the PPC is involved specifically in maintaining spatial information, as shown by sustained delay-period activity (reviewed in Curtis, 2006; Linden, 2007) and possibly in WM manipulation (Postle et al., 2006).

The PPC appears to work in concert with the PFC to solve the computations necessary for accurate spatial WM. The firing patterns of these regions is intrinsically linked: when cell populations in the dorsolateral PFC and lateral PPC cells were simultaneously recorded during a delayed saccade task, the neural activity patterns were shown to match (Chafee & Goldman-Rakic, 1998; Quintana & Fuster, 1999). Selective lesions to these regions in the macaque leads to a similar disruption in saccadic memory—saccades become less accurate as the delay period lengthens (reviewed in Curtis, 2006). Similarly, cortical cooling of either region while recording single-units in the other region showed that these regions have a strong interdependency during spatial WM tasks (Chafee & Goldman-Rakic, 2000). Similarly, TMS to either the PPC or dorsolateral PFC during spatial WM maintenance slows reaction times (Koch et al., 2005; Oliveri et al., 2001). Both regions are robustly activated during spatial WM tasks (Jonides et al., 1993; Smith & Jonides, 1998; reviewed in D'Esposito, 2007; Naghavi & Nyberg, 2005; Passingham & Sakai, 2004; Ungerleider et al., 1998; Wager & Smith, 2003).

In spite of these similarities, there are differences between the neural profiles associated with the PPC and the PFC. The mnemonic activity of PPC neurons, specifically neurons in area 7a, appears to be closely aligned with bottom-up attentional activity as PPC neurons fire to any salient stimuli, even when the it is behaviorally irrelevant and PPC neurons begin firing before PFC neurons under bottom-up attentional conditions, suggesting that this region detects and registers the spatial location of visually presented stimuli (Constantinidis & Steinmetz, 2005; reviewed in Constantinidis, 2006). In contrast, the mnemonic activity of lateral PFC and frontal eye field neurons may be more closely aligned with top-down attention as frontal neurons begin to fire before lateral intrapari-

tal neurons under top-down attentional conditions (Buschman & Miller, 2007).

4. Working memory for objects or object features

In contrast to the strong converging evidence linking the PPC to spatial WM functions, the evidence for functional links between the PPC and object WM is weaker. Neurons in macaque lateral intraparietal sulcus are responsive to object shape during the remember periods of delayed-match-to-sample tasks. Neuronal selectivity can be independent of eye movements, reaching, or object manipulation—or in other words, independent from spatial processing (Serenio & Amador, 2006; Sereno & Maunsell, 1998). Also, lateral intraparietal neurons exhibit delay activity to target color when it is behaviorally relevant (Toth and Assad, 2002).

In humans, BOLD activity in the IPS has been shown to titrate with the number of shapes and colors that can be held in memory over brief amount of time, suggesting that this region has some role in governing WM capacity (Macoveanu, Klingberg, & Tegner, 2006; Todd & Marois, 2004; Todd & Marois, 2005; Xu & Chun, 2006). This activity is not due to the number of items viewed at encoding, but rather to the number of items accurately maintained in WM, lending support to the idea that the function of the IPS is mnemonic, not perceptual (Todd & Marois, 2004). Converging evidence for these findings can be found in a small number of neuropsychological studies. We required subjects with or without right PPC damage to remember four sequentially presented colors, abstract shapes, or common objects over a short delay period and then make an old/new recognition decision. A sequential task in which all information was presented at central fixation was used to minimize spatial demands. The results showed that right PPC damage was associated with diminished WM performance across stimulus categories (Berryhill & Olson, 2008b); for face WM impairments see (Warrington & James, 1967). A subsequent study tested patients with bilateral parietal lobe damage on exactly the same

task. A similar pattern of deficits was observed (Berryhill & Olson, 2008a).

Unfortunately, the results of other studies cast some doubt on the robustness of these findings. Several patients with right PPC damage and neglect were tested on an object WM task and no deficits were observed (Pisella et al., 2004). Another study found that right PPC patients were impaired on object delay-match-to-sample tasks only when the probed dimension (object or spatial) was unpredictable (Finke, Bublak, & Zihl, 2006), hinting that the right PPC's role in WM may be attentional rather than mnemonic. One of the only TMS studies relevant to this question administered single TMS pulses during the maintenance period of an object WM task, but found no effect of unilateral or bilateral PPC stimulation on performance (Oliveri et al., 2001).

As a whole, the evidence suggests that object WM relies to some degree on an intact parietal lobe although several unanswered questions remain (see Box 1, question 1). The fact that there are discrepant findings is troubling, and the reason for this remains elusive, although we have observed that the manner in which memory is probed leads to different patterns of performance after parietal lobe damage. This finding hints that retrieval processes may be key to understanding the functionality of the PPC (Berryhill & Olson, 2008a; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Drowos, Berryhill, & Olson, accepted for publication). We expand on this topic in the next section.

5. Mechanistic role of the parietal lobe in working memory

The mechanistic role of the parietal lobe in WM is currently unknown. The neuroimaging literature has focused on WM maintenance and two hypothetical roles of the PPC in WM that have emerged are in the manipulation of information during WM maintenance (Champod & Petrides, 2007; Wendelken, Bunge, & Carter, 2008), and in total information accumulation during WM maintenance (Xu, 2007). In contrast, the neuropsychological literature has offered the hypothesis that the PPC's role in WM is in instantiating particular retrieval processes (Berryhill & Olson, 2008a).

5.1. Information manipulation hypothesis

Several investigators have proposed that the mnemonic function of the PPC is specifically associated with the manipulation of information held in WM (Champod & Petrides, 2007; Wendelken et al., 2008). For instance, in one recent study subjects were required to remember letters and colors under several different conditions. In the *low* and *high* memory load conditions, the task was to remember the alphanumeric items in the memory set and respond whether two probe items had been present in the preceding memory set. In the *organization* condition, the task was to remember whether the probe items had been previously shown in the same color. In their second experiment, the organization task was to spatially reorganize the items according to arrows. In both studies, the authors observed frontal activity (DLPFC, VLPFC) during the delay period associated with WM load. However, superior parietal activity (BA 7) was only observed when WM maintenance required manipulation (Wendelken et al., 2008). Similar SPL regions are activated during other tasks demanding item reorganization in WM such as order sequencing tasks (Marshuetz & Smith, 2006; Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000; Wager & Smith, 2003), and mathematical calculation tasks (Dehaene, Molko, Cohen, & Wilson, 2004; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). One problem with this interpretation is it does not account for the large number of WM studies in which the task

does not include a manipulation requirement, yet SPL activations are observed. Also, the manipulation hypothesis falls prey to the "difficulty explanation", that greater PPC activations in the manipulation condition are simply due to the greater difficulty of that task compared to the baseline condition.

5.2. Information load hypothesis

Behavioral studies have shown that on average, most people can maintain approximately four objects in visual WM (Luck & Vogel, 1997) and that memory capacity varies with the complexity (Alvarez & Cavanagh, 2004), or with the similarity of these items (Awh, Barton, & Vogel, 2007; Olson & Jiang, 2002). Interestingly, portions of the parietal lobe appear to be sensitive to memory capacity limitations. In one study, subjects observed an array of colored squares and after a brief delay, were shown a probe image and made a same/different judgment. In a whole brain analysis, only one region titrated with memory capacity: the superior IPS. Note that superior IPS activity was not modulated by set size but rather, the number of objects that subjects could accurately maintain in memory such that neural activity leveled off as memory capacity reached asymptote. Additional analyses revealed that activity correlated with individual performance on the object WM task (Todd & Marois, 2004, 2005). This finding and those of others (Xu & Chun, 2006) suggest that one role of the superior IPS in WM is to maintain a finite number of objects over short delay periods.

An alternative explanation is that the superior IPS maintains visual features, rather than discrete objects, over a short period of time. Note that the number of objects and visual features are highly correlated in most studies using visual stimuli. To understand their individual contributions, Xu (2007) dissociated feature and object information. In her study, subjects were required to remember stimulus arrays with the same number of objects (all black shapes) but different numbers of features (variably colored shapes). In a separate task, the number of objects was varied, but the number of features remained constant. The results showed that the superior IPS exhibited greater changes in signal strength when there were more visual features present. However, there was no difference in the superior IPS when the number of objects was varied, holding the number of features constant (Xu & Chun, 2006; see also Xu, 2007). This finding provides evidence for the view that the superior IPS represents the sum total of perceptual information stored in WM.

These findings predict that superior IPS damage will diminish visual WM capacity, as a function of the number of visual features of the items. We tested this prediction in two studies by requiring patients with unilateral or bilateral parietal lobe damage to remember visual stimuli that varied in the number of features: color patches, novel shapes, and common objects. The first part of the prediction was supported: visual WM capacity was diminished after PPC damage. However, the second part of the prediction was not borne out in these data: there was no effect of stimulus complexity or number of features on patient performance (Berryhill & Olson, 2008a, 2008b), suggesting that visual feature load does not fully explain the mechanistic function of the PPC in WM.

5.3. Retrieval process hypothesis

In a series of WM studies, we examined the role of the PPC in WM while manipulating the retrieval process. The performance of two patients with bilateral parietal damage was compared to that of matched controls (Berryhill & Olson, 2008a). In the first pair of experiments, order WM was tested with either recall or recognition retrieval probes. Subjects observed four

sequentially presented items (colors, shapes, or objects) and after a brief delay, the same items were repeated. The recognition task was to make a same/different judgment regarding the order of the four items. In the recall version, a single probe item appeared after the delay and the task was to provide the ordinal position (1–4) of that image. The patients exhibited impaired WM performance when probed by old/new recognition, but intact WM performance when probed by recall. In a second pair of studies, the task was to remember the identity of four common objects over a brief delay, and then to make either an old/new judgment or to verbally name the objects that had been shown. The same pattern of preserved recall accompanied by impaired recognition was observed (see Fig. 2). These findings cannot be attributed to deficient encoding or maintenance processes because these demands were held constant; only the retrieval process varied. This finding leads us to suggest that the PPC's role in WM is specifically linked to retrieval processes. If true, this function coincides with a wealth of findings on retrieval in the episodic memory literature, discussed next.

6. Episodic memory

Findings linking episodic memory to the parietal lobe have recently aroused considerable attention from the cognitive neuroscience community. Several excellent reviews of this topic are available and we direct interested readers to these sources (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Simons & Mayes, 2008), see also Uncapher & Wagner, this volume; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). To summarize: parietal activity is greater when an old stimulus is correctly identified as old, compared to when a new item is correctly identified as new. The benefit afforded stimuli retrieved as old is extended to items that were *incorrectly* perceived as old (Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003). Separable regions in the lateral parietal lobe, a superior and an inferior region, show complementary patterns of activity; the superior area appears to reflect top-down influence in mediating low-confidence responses and the inferior region reflects bottom-up influence mediating high-confidence responses (Kim & Cabeza, 2007).

Until recently, these findings were viewed with skepticism because they suffered from an absence of converging evidence from other techniques. A key piece of converging evidence was recently provided by a study of patients with bilateral parietal lobe lesions (lesions are shown in Fig. 2A). In this study, patients and matched controls were asked to recollect various autobiographical memories. In condition 1, they freely recalled events from their lifetime in as much detail as possible. In condition 2, they answered specific questions about these memories. The results showed that parietal lobe damage decreased the vividness and amount of detail freely recalled. However, when patients were probed for specific details pertaining to their memories, they performed normally (Berryhill et al., 2007; see also Hunkin et al., 1995). We recently tested the same patients on the Deese–McDermott Roediger (DRM) false memory paradigm and found that they exhibited normal false memory when tested by recall and impaired levels when tested by old/new recognition (see Fig. 2). Interestingly, they also exhibited an abnormally low level of “remember” responses compared to “know” response (Drowos et al., accepted for publication) (see Fig. 2).

7. Mechanistic role of the parietal lobe in episodic memory

A large number of fMRI studies have reported that portions of the PPC are modulated as a function of episodic memory retrieval demands. We do not discuss these findings in detail as they have been thoroughly reviewed elsewhere (Cabeza, 2008; Naghavi & Nyberg, 2005; Wagner et al., 2005). Suffice it to say that these findings come from a number of different laboratories using different tasks and stimuli, making a compelling case for PPC involvement in episodic memory retrieval. Discerning what exactly that role might be is the subject of much current investigation. Suggested roles include serving as an episodic buffer, a type of WM (Baddeley, 2000; Vilberg, Moosavi, & Rugg, 2006; Vilberg & Rugg, 2008), providing an assessment of memory signal strength, as a mnemonic accumulator (Wagner et al., 2005), in directing internal attention (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008), or as a gauge of memory subjectivity or confidence (Ally, Simons,

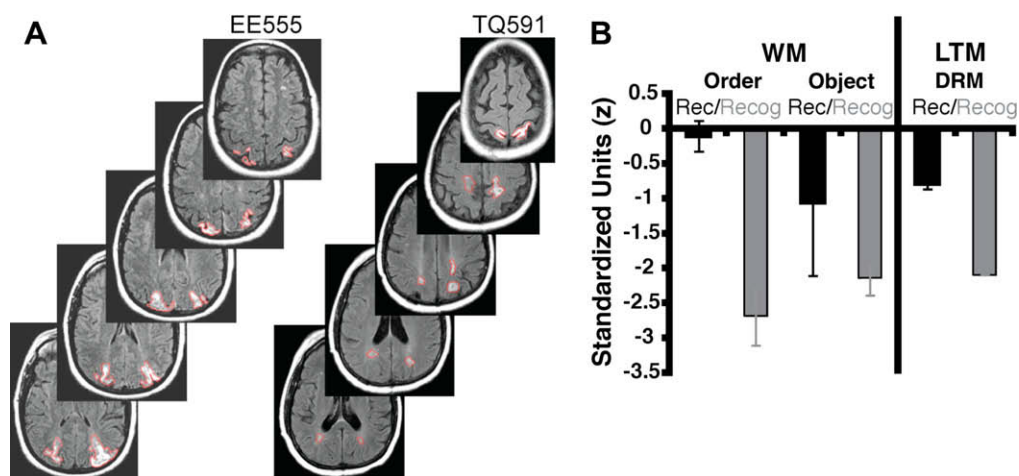


Fig. 2. Parietal lesions and working memory, episodic memory performance. (A) Working memory and episodic memory was investigated in two patients with bilateral parietal lobe lesions. MRI images show the lesions outlined in red. (B) Three experiments spanning short and long-term forms of memory probed memory with two different response tasks. In order and object WM (left), recall (Rec) performance was preserved whereas recognition (Recog) performance was impaired (Berryhill & Olson, 2008a). In a long-term memory (LTM) task, performance was assessed with the DRM paradigm, and the same pattern of preserved recall and impaired recognition performance was observed (Drowos et al., 2008, accepted pending revisions). Data are shown as standardized scores in which performance greater than 1.96 standard deviations is considered impaired.

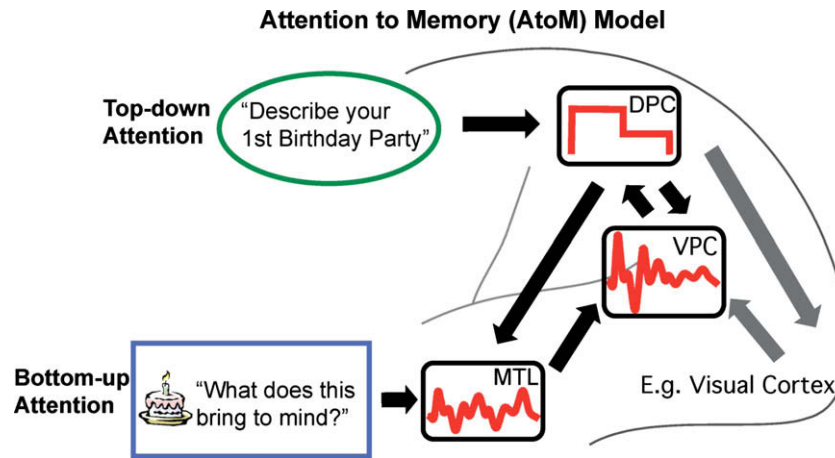


Fig. 3. The attention to memory (A to M) model proposes two loci of parietal involvement in memory retrieval that map onto two forms of attentional demands (Cabeza et al., 2008). Top-down attention is controlled and sustained by neurons in the superior or dorsal parietal cortex (DPC). The DPC directs attention towards a retrieval goal, in this case, the memory of a 1st birthday party. In contrast, bottom-up attention can be captured by environmental stimuli or by sensory cues, such as the image of the birthday cake. In this case, the medial temporal lobes (MTL) cause the inferior or ventral parietal cortex (VPC) to signal the DPC to attend to the spontaneously retrieved memory. The waveforms reflect the variability in retrieval demands.

McKeever, Peers, & Budson, 2008; Simons, Peers, Mazuz, Berryhill, & Olson, submitted for publication).

Our episodic memory findings, reviewed earlier, also point towards memory retrieval processes being disrupted after PPC damage in that episodic memory is impaired under some, but not other, retrieval conditions (Berryhill et al., 2007; Drowos et al., accepted for publication). Preserved memory on several episodic memory tasks, in studies conducted by ourselves and others (Davidson et al., 2008; Simons et al., 2008a; Simons et al., submitted for publication) indicate that memory retrieval per se is not diminished by parietal lobe damage, but rather a particular subprocess that is tapped in some tasks but not others.

One proposed hypothesis that appears to offer a happy marriage between the WM findings reviewed earlier, and episodic memory findings is that portions of the PPC serve as the interface between WM and episodic memory retrieval—as the episodic buffer (Baddeley, 2000). According to this hypothesis, the retrieval of greater amounts of integrated multi-modal information causes subjects to have confidence in their retrieval judgments and increases the maintenance demands on the episodic buffer. This hypothesis can explain many of the findings in the visual WM literature, such as increased BOLD activations with recollected rather than familiar memories (Daselaar, Fleck, & Cabeza, 2006; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005; reviewed in Skinner & Fernandes, 2007), and decreased WM capacity after PPC damage (Berryhill & Olson, 2008a, 2008b). However, it fails to explain why PPC damage leads to different levels of memory performance depending on the probe task (Cabeza et al., 2008).

A second proposal suggests that portions of the PPC assess the strength of a memory signal in order to determine whether a stimulus was previously viewed. This mnemonic accumulator hypothesis (Wagner et al., 2005) can be easily understood as an analogy to signal detection theory in which evidence is accrued and some criterion level is set. This view is unable to explain why different memory tasks produce different response patterns in the parietal cortex, as some sort of signal estimate should be resistant to the type of information retrieved (reviewed in Cabeza, 2008).

A third possibility is that the PPC's role in memory retrieval parallels its role in attention (Cabeza, 2008; Cabeza et al.,

2008; Wagner et al., 2005). To understand how this may work it is important to understand that attention and memory are tightly intertwined at nearly every stage of mnemonic processing (reviewed in Awh, Vogel, & Oh, 2006; Chun & Turk-Browne, 2007; Naghavi & Nyberg, 2005). They are linked at encoding because top-down attention to any given item improves the perception of features, such as contrast (Carrasco, Ling, & Read, 2004). Selective attention acts as a gatekeeper, filtering which aspects of the environment are encoded into memory, and which items are not. Attention and memory are also intertwined during memory maintenance as demonstrated by the fact that distraction during delay periods disrupts memory performance. Last, attention may be needed for accurate retrieval because divided attention tasks can cause interference and failures of retrieval even for items that were encoded with full attention (Fernandes & Moscovitch, 2000). As originally conceived, the attention to internal representation hypothesis suggested that the parietal lobe focused attention on items held in memory (Wagner et al., 2005). This hypothesis has been expanded from a purely goal driven, or top-down, attentional modulation to include spontaneous, or bottom-up, attentional modulation, which maps onto dorsal and ventral parietal regions (Cabeza, 2008). The most recent version of this expanded view, the *attention to memory model* (AtoM) suggests that memory goals can be allocated deliberately (top-down) or can be captured by a memory cue (bottom-up) (see Fig. 3). Explicit directions provide a goal to guide internal memory retrieval towards a particular memory. This process is sustained by a region in the BA 7 of the superior parietal lobe. In contrast, a memory may be spontaneously evoked by an environmental stimulus in a bottom-up fashion. When this happens, the MTL connections with inferior parietal lobe regions cause the superior parietal region to redirect attention to the bottom-up driven recollection.

This hypothesis can explain much of the episodic memory literature, including our findings in which bottom-up, spontaneous retrieval of autobiographical memories was impaired in patients with bilateral ventral parietal damage, but top-down, cued retrieval was normal (Berryhill et al., 2007). One neuropsychological finding fails to support this model; however, we found that diminishing top-down attention cues to the critical feature that was later tested in an auditory source memory task had little effect on the source memory performance of patients

with bilateral PPC damage (Simons et al., submitted for publication).

The last hypothesis we discuss, the subjective memory hypothesis proposes that the parietal lobe is responsible for the subjective experience of confidence and vividness in one's retrieved memories (Ally et al., 2008). This hypothesis finds support in a small number of neuroimaging findings (Chua, Schacter, Rand-Giovannetti, & Sperling, 2006; Durate, Henson, & Graham, 2008), in statements made by parietal patients that they had diminished vividness and confidence in their memory abilities (Ally et al., 2008; Davidson et al., 2008), and in neuropsychological findings showing decreased levels of memory confidence (Davidson et al., 2008; Drowos et al., accepted for publication; Simons et al., submitted for publication), and memory vividness (Berryhill et al., 2007). Interesting, several years ago Hunkin and colleagues reported on a patient, DH, who had parieto-occipital damage due to a closed head injury. This patient had semantic memories for his lifetime but he felt that he lacked "genuine" memories of this life. He claimed that he did not feel that he had truly experienced these memories: "He said it was as if he had read a book about his life but he did not confuse these facts with real memories any more than one would confuse a story in a book with real life" (Hunkin et al., 1995). Again, this finding supports the contention that the parietal lobe may have a special role in eliciting or interpreting subjective memory states.

These reports are reminiscent of findings in the hemispatial neglect literature indicating that portions of the parietal lobe (right inferior) play a role in subjective states of awareness. Perhaps it is the case that the inferior parietal lobe plays an analogous role in awareness, and hence confidence, of memories.

8. Conclusions

The functionality of the PPC, like that of the frontal lobe, cannot be characterized as simply sensory, motor, or cognitive. Parietal functions that were identified generations ago in lesion studies—spatial attention, visual guidance of action (eye movements, grasping), calculation, reading—do not appear to have an underlying categorical structure that provides for easy analysis. Complicating the situation, in this paper we suggest that an additional function should be added to this list: memory retrieval.

Our review indicates that (1) the PPC plays a critical role in spatial working memory. (2) The PPC may also have a role in object WM, although this role remains less substantiated. (3) The PPC's role in WM may be most strongly linked to memory retrieval (Berryhill & Olson, 2008a). (4) The PPC plays an important role in episodic memory retrieval, although encoding functions may also exist (see Uncapher & Wagner, this volume). Links between the posterior parietal lobe and memory retrieval were first noted in fMRI studies of episodic memory. More recently, lesion studies indicate that PPC damage can cause selective retrieval difficulties in the context of episodic retrieval tasks. (5) Many mechanistic accounts of the PPC's role in episodic memory have been proposed. Two accounts that find agreement with much of the existing data are the attention to memory (AtoM) hypothesis (Cabeza et al., 2008) and the subjective memory hypothesis (Ally et al., 2008).

The goal of this review is in part to raise interest in these remaining questions and to provoke researchers to develop clearly testable hypotheses (see Box 1). The prospect of answering these questions is certain to drive the field of memory research in the years to come.

Box 1 Question for future research

- [1] Given that a hallmark of parietal functioning is spatial selectivity, is object WM truly independent from spatial processing functions of the PPC? According to one view, whenever we encode objects, we automatically encode and maintain stimulus location, even when location is task irrelevant (Jiang, Olson, & Chun, 2000). In support of this finding, macaque research indicates that PPC coding is largely retinotopic even in object WM tasks and that IPS neurons are more sensitive to remembered locations than remembered objects (Sabes, Breznen, & Andersen, 2002). The object attributes to which IPS neurons are most sensitive—shape and size—are inherently spatial in nature. However, the inter-species generalizability of these findings is poorly understood.
- [2] Are the parietal mechanisms for attention and memory encoding one and the same? According to one view, PPC activations during WM tasks simply represent attention to objects (Cowan, 2001; Majerus et al., 2007). In support of this view, a recent fMRI study probed set-size effects during an object WM task and two control tasks of perceptual attention, finding similar IPS activity and limitations during all tasks (Mitchell & Cusack, 2008). Because the attention task had no WM requirements, the authors suggest that the activity reflects the processing of attended items.
- [3] Can different mnemonic processes be linked to different parietal lobe regions? Episodic memory *retrieval* has been associated with IPL activations, while visual working memory *maintenance* has been associated with IPS activations. Expected laterality differences—left PPC for verbal material, right PPC for visual material—have seldom been reported in fMRI studies, although they are commonly reported in neuropsychological studies.
- [4] Our neuropsychological findings showed a dissociation between WM recall and recognition such that parietal lobe damage only adversely affected recognition. A similar dissociation has not been reported in long-term memory tasks and indeed, several studies have reported normal levels of recognition memory after parietal lobe damage (Davidson et al., 2008; Simons et al., 2008a, submitted for publication). Are recall and recognition differentially reliant on the parietal lobe at different time scales?

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